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F. B. MUMFORD, *Director*

# GROWTH AND DEVELOPMENT

*With Special Reference to Domestic Animals*

## XLIV. Energetic Efficiency of Egg Production and the Influence of Live Weight Thereon.

SAMUEL BRODY, E. M. FUNK, AND H. L. KEMPSTER

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## CONTENTS

	Page
I. Introduction .....	5
1. Orientation .....	5
2. Definitions .....	7
a. Gross energetic efficiency of egg production .....	7
b. Net energetic efficiency of egg production .....	9
c. Partition of nutrients for various uses .....	9
II. Data .....	11
III. Method of analyzing the data .....	13
IV. Results of analysis of original data .....	17
1. Average and maximum efficiency of egg production .....	17
2. Data and equation inferences .....	18
3. Net efficiency of egg production .....	18
4. Gross efficiency of egg production .....	19
5. Comparison of energetic efficiencies of egg and milk production .....	20
A. Comparison of energetic efficiencies of "ordinary" fowls, cows, and rats .....	20
B. Comparison of energetic efficiencies of "extraordinary" fowls and cows .....	22
C. Physiologic significance of efficiency differences be- tween egg and milk production .....	24
(a). The organizational complexity aspects .....	25
(b). The time factor .....	26
6. Body weight vs. efficiency .....	30
V. Analysis of published data .....	33
1. Efficiency levels .....	33
2. Influence of production level on efficiency .....	35
3. Influence of body weight on production level and gross efficiency .....	37
a. Egg weight vs. body weight .....	37
b. Egg number and production vs. body weight .....	42
4. Influence of feed consumption level on efficiency of egg production, and of egg production level on feed consumption .....	46
5. Comparison between egg production and growth ef- ficiency .....	48

VI. Summary and conclusions .....	51
VII. Appendix .....	53
A. Table A, summarizing original data, equation constants, and related items .....	54
B. Table B, a tentative "feeding standard" for fowls .....	56
C. Seasonal and age course of energetic efficiency of egg pro- duction, represented in Fig. 12, based on data col- lected in this Station .....	57
D. Seasonal course in energetic efficiency of egg production represented in Figs. 13a and 13b, based on Utah Egg-laying contest data .....	58
E. Interrelation between efficiency and profit represented in Fig. 14 .....	59

## FOREWORD

The special investigation on growth and development is a cooperative enterprise in which the departments of Animal Husbandry, Dairy Husbandry, Agricultural Chemistry, and Poultry Husbandry have each contributed a substantial part. The parts for the investigation in the beginning were inaugurated by a committee including A. C. Ragsdale, E. A. Trowbridge, H. L. Kempster, A. G. Hogan, F. B. Mumford. Samuel Brody served as Chairman of this committee and has been chiefly responsible for the execution of the plans, interpretation of results and the preparation of the publications resulting from this enterprise.

The investigation has been made possible through a grant by the Herman Frasch Foundation, now represented by Dr. F. J. Sievers.

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## ABSTRACT

(1) Fowls produce most eggs at a characteristic body weight which is about 4 pounds in Leghorns and about 5½ pounds in Rhode Island Reds and Barred Rocks. Preceding these body weights of maximum production, gross energetic efficiency of egg production tends to be independent of body weight; following these body weights, gross energetic efficiency decreases. (2) The *gross* energetic efficiency of egg production (ratio of

egg energy produced to TDN energy consumed) is of the order of 11% in 100-egg producers, 14% in 150-egg producers, 17% in 200-egg producers, 20% in 250-egg producers, 27% in 360-egg producers. These are *very* rough estimates depending on size of egg, size of fowl, nature of feed, and on other factors which have not been defined. In these computations it was assumed, on the basis of an analysis of a dozen 58-gram eggs, that the fuel value of one gram of whole egg including shell, is 1.6 Calories (kilocalories). The value per gram of air-dry feed was assumed to be 3 Cal. TDN. The investigation leads to the conclusion that the gross energetic efficiency of egg production in "good" layers is about  $\frac{1}{3}$  that of the efficiency of milk production in "good" milkers, and about the same as the efficiency of early postnatal growth. (3) The distribution of the consumed feed between its uses for egg production, maintenance, and weight gain (or loss) was found to be represented (*for an extremely low-producing group*) by the equation,  $\text{Feed} = 0.692 (\text{egg}) + 0.30 M^{0.73} \pm 1.1 \Delta M$ . This equation assumes that maintenance varies with the 0.73 power of body weight, and the equation indicates that: maintenance cost per  $M^{0.73}$  is 0.30 units of feed; production cost per unit weight of egg, 0.692 unit feed; production cost per unit change in body weight is 1.1 unit feed. Thus, 0.692 grams, or 2.18 Cal. ( $= 0.692 \times 3$ ) of feed was expended for producing 1 gram, or 1.6 Cal. egg so that the *net* efficiency (not counting maintenance) is roughly  $\frac{1.6}{2.1}$  or about 76%. Other data showed the net efficiency to be about 60%. It appears from these incomplete data and computations that *the net efficiency of egg production (not counting maintenance) is perhaps of the same order as of milk production, but that the gross efficiency of egg production (including maintenance of fowl) in "good" layers is only about half the efficiency of milk production in "good" dairy cattle.* (See Table 1 for a comparison of gross efficiencies of production in fowls, dairy cattle, and in a rat.)

The difference in gross efficiency of egg and milk production is attributed to four factors: (1) There is greater structural complexity (with consequently greater energy cost of organization which can not be measured calorimetrically) in egg than milk. (2) As a result of (1) more "biologic time" is taken to produce unit egg energy than unit milk energy, with consequently greater expenditure of overhead maintenance cost per calorie of egg than milk. (3) Egg contains relatively more fat (produced from a predominantly carbohydrate diet) than milk, with consequently greater energy expense for producing an egg calorie than a milk calorie. (4) Evolution apparently favored increasing milk production to a greater extent than egg production, with corresponding greater digestive and metabolic powers in cows than fowls. Increasing the number of reproductive systems in fowls so as to make them quantitatively comparable to the four quarters of the cow's udder, would probably not increase the production level because of the limiting effect of the digestive and metabolic systems which were probably adopted in the course of evolution to support only one reproductive system.

The gross energetic efficiency of egg production is less than of early postnatal growth and very much less than of prenatal growth in the chick. The reasons for this difference are discussed in the text.



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## I. INTRODUCTION

### 1. Orientation

One of the most intriguing problems in agricultural energetics concerns the relative efficiency of energy transformations in different types of agriculturally productive processes. What are the relative energetic efficiencies of growth, of milk production, of egg production, of muscular work? Are the average and maximum efficiencies of egg production in domestic fowls greater or less than the average and maximum energetic efficiencies of milk production in dairy cattle, muscular work in horses, growth in all classes of farm animals?

There are certain limits which energetic efficiency can not exceed, and it would obviously be wasted time to attempt to increase efficiency beyond these levels by breeding or hormone techniques. We have thus shown<sup>1</sup>, on the basis of our own work and on the basis of the results of Hill and others, that the overall efficiency of muscular work in horses can not exceed 25%; that the *average overall* energetic efficiency of milk production<sup>2</sup> with respect to consumed TDN is in "good" experiment station dairy cattle of the order of 30% and that the maximum efficiency is of the order of 48%; that the overall energetic efficiency of growth declines with increasing age, but is of the order of 30% in early postnatal life. Now what is the average and maximum overall energetic efficiency of egg production?

Fascinating also is the biological problem relating to the amount of energy expended for, or "work" performed in, the various biologic transformations, and especially the work involved in transforming of biologically unorganized into organized matter, of nonliving matter into living organisms. Bricks are the same before and after they are made into a house, but their arrangement in the form of a house requires work and involves considerable energy expenditure. Likewise, the building units in the egg are probably the same before and after they are made into a chick, but their rearrangement from

<sup>1</sup>Missouri Agr. Exp. Sta. Res. Buls. 209, 1934; 244, 1936, and Missouri Sta. Bul. 383, 1937.

<sup>2</sup>Missouri Agr. Exp. Sta. Res. Buls. 222, 238, and 239.

positions in the egg to those in the chick—the transformation from non-living to living—must involve an energy cost. What is the price—what is the energy cost—of becoming organized, especially organized into a living being<sup>3</sup>, of crossing from the realm of non-living egg into living chick? We do not know, in spite of the romantic quest of a brilliant array of investigators beginning in 1903 with Tangl in Budapest and Bohr in Copenhagen<sup>4</sup>.

Tangl was optimistic about his ability to solve this problem because he oversimplified it. He thought all he would have to do to determine the work, the energy cost, of organizing the chick embryo from the egg, would be to burn in a bomb calorimeter eggs at the beginning and end of incubation; the difference in energy content would represent this work or energy cost of producing a chick from an egg.

One fallacy in Tangl's reasoning is that the energy disappearance from the egg as thus measured includes not only the cost of organizing the chick from the egg, but also the cost of maintaining the formed embryo. He failed to differentiate growth cost from maintenance cost. It is interesting to note that Eckles, in Missouri<sup>5</sup>, likewise oversimplified a similar problem, but in the opposite direction. Eckles assumed that the energy content of the new-born calf represents the energy expended by its mother in producing it; he overlooked the energy cost of maintenance.

A second fallacy in Tangl's reasoning is due to his ignoring the fact that before the chick embryo is burned in the calorimeter it is necessarily killed and dried. The killing and drying, of course, not only returns the living to the non-living state but also destroys the physico-chemical arrangement of molecules constituting normal living chick embryo. The energy cost of becoming alive and organized disappears in the process of dying and drying before the burning stage is reached. Tangl therefore missed what he was looking for, namely the energy of organization of the embryo and the energy of becoming alive.

The problem of "work" of growth is a part of the more general problem of "work" of other productive functions such, for example, as the "work" involved in producing the egg from its precursors in

<sup>3</sup>A classic paper on this problem is by Emile F. Terroine and René Wurmser, entitled, *L'énergie de croissance I. Le développement de l'aspergillus niger*. *Bul. Soc. Chim. Biol.*, 4, 519, 1922, which perhaps introduced the notion of raising the chemical potential during growth as indicated by the quotation ". . . il doit en même temps exercer un travail contre l'extérieur et surtout dans la plupart des cas élever le potentiel chimique des substances dont il dispose il y a donc là besoins d'énergie."

<sup>4</sup>The best review of the problem, with particular reference to the historical aspects is given by Joseph Needham's *Chemical Embryology*, Vol. 2, pp. 946-999 (Cambridge 1931).

<sup>5</sup>Eckles, C. H. The nutrients required to develop the bovine fetus. *Missouri Agric. Exp. Sta. Res. Bul.* 26, 1918.

the blood and from the food. What is the energy cost of transforming and rearranging the ultimate building units from food into egg precursors in the blood, and into egg? We do not know. Our ignorance is due to the complexities of the process as indicated by the following outline, discussed in terms of energetic efficiency of transformation of food into egg.

## 2. Definitions

Energetic efficiency is the ratio of energy of output to energy of input, thus:

$$\text{Efficiency} = \frac{\text{Output}}{\text{Input}} = \frac{\text{Energy in the given product}}{\text{Energy expended to produce the given product}} \quad (1)$$

a. **Gross energetic efficiency of egg production.**—In the case of egg production, the overall or *gross* energetic efficiency may be defined by the equation:

$$\text{Gross Efficiency} = \frac{\text{Energy in egg produced during given time}}{\text{Energy in feed consumed during the same time}} \quad (2)$$

The physical—as contrasted to the biologic and organizational—energy of the output, egg, is clearly defined: It is the combustion value of the egg as burned in a bomb calorimeter.

The physiological energy value of the input, the feed, is not thus clearly defined. It varies with the plane of nutrition, with the balance between the nutrients, with the condition and individuality of the bird, and with the reference bases employed. The energy of the feed may be referred to in terms of: (1) total energy; (2) digestible energy; (3) metabolizable energy; (4) net energy. Each of these has a different significance, and is differently influenced by the factors listed above.

Roughly defined, *digestible energy*, or TDN, is total energy less fecal energy. *Metabolizable energy*, is the digestible energy less urinary energy. *Net energy* is metabolizable energy less the heat increment of feeding (specific dynamic action). The heat increment varies enormously with the plane of nutrition and with the balance among the nutrients in the ration.

In computing the efficiency of a process such as egg production, the numerical value of the efficiency will vary with the form of the food to which the product—egg—is compared. It is clear from equations (1) and (2) above that the computed efficiency will be greater if the energy of the egg is compared to the *digestible* energy

than to the *gross, or total energy* in the feed; still greater if compared to the *metabolizable energy*; and still greater if compared to the *net energy*.

We can not employ net energy values for computing efficiency of egg production because, as is now generally known, the net energy, or availability, of a ration for productive purposes varies with the balance among the several constituents in the diet. In the words of Mitchell<sup>6</sup>, "the utilization of metabolizable energy is primarily a function of the nutritive balance existing among the nutrients of the ration." Moreover, because of the difficulty of separate collection of urine and feces in birds, little is known about metabolizability and digestibility of feeds in birds. On the other hand, for our purpose of comparing energetic efficiencies of egg production with milk production and with growth, it would be confusing to compute efficiency on the basis of gross or total energy of the feed, because feeds used by the several species vary tremendously in digestibility. For this reason it seems most reasonable from the comparative viewpoint to compute efficiency of egg production with regard to "TDN", or "total digestible nutrients". Unfortunately, the digestibility values that we shall use were obtained not in digestion trials with birds, but with farm animals, as explained in Morrison's *Feeds and Feeding*<sup>7</sup>.

We shall define energetic efficiency of egg production with reference to the digestible nutrients, or TDN, as given by Morrison<sup>7</sup>, without implying that it is proper to use Morrison's tables for digestibility values in birds. The definition is given by the equation

$$\frac{\text{Gross Energetic Efficiency}}{\text{Efficiency}} = \frac{\text{energy in eggs produced}}{\text{energy in TDN consumed}} \quad (3)$$

in which the energy in the egg is the bomb-calorimeter combustion value of the egg sample; the energy in the TDN is assumed to be 4 Cal. per gram or 1814 Calories per pound; the TDN values for the feed were computed from Morrison's tables<sup>7</sup>.

Replacing the egg and the TDN energies by their numerical equivalents, we obtain the equation

$$\frac{\text{Gross Energetic Efficiency}}{\text{Efficiency}} = \frac{1.6 \times \text{gms. eggs}}{3 \times \text{gms. feed}} \quad (4)$$

in which 1.6 is the caloric equivalent of 1 gm. of whole egg (including shell), and 3 is the caloric equivalent of the TDN in a gram of feed.

We should say that on the average the eggs laid by our group of birds weighed 54.76 grams per egg, but that the eggs that we burned

<sup>6</sup>Mitchell, H. H., Report of the Conference on Energy Metabolism, Committee on Animal Nutrition, National Research Council, 1935. See also Forbes, E. B., *Science*, 77, 306, 1933.

<sup>7</sup>Morrison, F. B., *Feeds and feeding*, Ithaca, New York, 1936.

in the bomb calorimeter weighed on the average 58.01 grams. In terms of whole egg instead of grams of egg the above equation would be

$$\text{Gross efficiency} = \frac{1.6 \times 54.76 \times \text{number eggs laid}}{3 \times \text{gm. feed}} \quad (5)$$

To summarize, *gross* energetic efficiency of egg production is the ratio of the total energy in the egg to the energy in the TDN of feed consumed.

**b. Net energetic efficiency of egg production:** *Net* efficiency differs from *gross* efficiency in not including in the reference base the energy cost of maintenance of the animal. While *gross* energetic efficiency is the ratio of the energy in the egg to the energy in the TDN consumed, *net* energetic efficiency is the ratio of the energy in the egg to the energy in the feed consumed less that part of the feed used for maintenance, and of course less that part of the feed used for gaining (or losing) body weight.

$$\text{Net energetic efficiency of egg production} = \frac{\text{energy in eggs produced}}{\text{energy in TDN less TDN expended for maintenance and for live weight gains.}} \quad (6)$$

**c. Partition of nutrients for various uses:** The food energy consumed by the bird is expended for various purposes including: (1) gains (or losses) in body weight; (2) storing energy in the egg; (3) maintaining the bird (not including the active reproductive system); (4) maintaining the active reproductive system alone; (5) *work* of egg secretion; (6) increased metabolic level of the bird due to stimulating influence of reproductive precursors and hormones; (7) wastes incidental to the transformation into eggs of egg precursors.

This enumeration indicates that the *work* of egg production is only one of at least eight items in the total cost of egg production.

It is *theoretically* possible to evaluate some of these items separately. Thus the energy expended by the reproductive system for transforming egg precursors into egg may be evaluated—given the skill and apparatus—by measuring: (1) blood flow through the active reproductive system; (2) O<sub>2</sub> decrement of the blood in its passage through the reproductive system; (3) CO<sub>2</sub> increment in this passage. These data would enable computing the energy expense of transforming egg precursors into egg (i.e., *work* of egg secretion), including however, the *maintenance cost of the reproductive system*. Such an evaluation assumes that the O<sub>2</sub> decrement is not greatly complicated by changes in O<sub>2</sub> concentration due to interconversion of fats and

carbohydrates in the process of egg production. In other words, such data would resemble Tangl's data on embryo growth in that they would be complicated by a maintenance factor. There appears to be no direct method for separating the maintenance cost of a productive organ from the production cost. This is an aspect of the unsolved problems of evaluating the energy cost of organization.

It is also theoretically possible to measure the energy expended by the reproductive system of heavy laying hens for "making" eggs by comparing the metabolism of the anesthetized bird before and after excluding the reproductive system from the circulation by ligating the principal blood vessels. But there are many evident objections against such procedure.

While awaiting the direct evaluation of energy expenditure by laying birds for each of the aforelisted functions, it may be possible to partition the TDN by an indirect mathematical method. Thus it is legitimate to assume, by way of first approximation, that the consumed available food energy must equal the algebraic sum of the energies of egg produced, "work" of converting egg precursors into egg, maintenance cost of the laying bird, and gain (or loss) in live weight.

The above assumption may be summarized by the "partition equation"

$$\text{TDN} = A + B(\text{egg}) + C M^{0.73} + D \Delta M \quad (7)$$

in which TDN represents total digestible nutrients (Morrison); *A*, a parameter constant; *egg*, represents egg weight of given composition; *M*, live weight;  $\Delta M$ , gain (or loss) in live weight; *B*, units TDN required for producing unit egg weight; *D*, units TDN required for gaining unit live weight; *C*, units TDN required to maintain unit "physiologic mass" (the 0.73 power of body weight).

The reason for raising weight to the 0.73 power in the maintenance term is that it was previously shown in Missouri Research Bulletins 166 and 220 that basal energy metabolism and endogenous nitrogen excretion in mature animals tends to be proportional not to simple body weight but to the 0.73 power of body weight. Until evidence is produced to the contrary, it is reasonable to assume that maintenance also tends to vary with the 0.73 power of body weight in mature animals of the same species.

## II. DATA

The data on feed consumption, egg production, body weight, and body weight gains which we shall analyze with the aid of equation (7) were secured on a total of 289 birds, 174 White Leghorns and 115 Rhode Island Reds, during the course of three years (1934-7). A total of 2524 28-day observations were made, including 1429 periods on White Leghorns and 1095 periods on Rhode Island Reds. However, some of the periods were incomplete and were omitted, with the result that the following efficiency computations are based on 2237 28-day periods.

The birds were kept in individual compartments in laying batteries. Each compartment was supplied with a feeding box containing the following all-mash mix:

Ground corn, 35 pounds	.....	29.3 lbs. TDN*
Ground wheat, 20 pounds	.....	15.68 lbs. TDN*
Ground oats, 15 pounds	.....	10.73 lbs. TDN*
Wheat bran, 10 pounds	.....	7.02 lbs. TDN*
Alfalfa leaf meal, 5 pounds	.....	2.86 lbs. TDN*
Meat scraps, 8 pounds	.....	5.46 lbs. TDN*
Dried buttermilk, 5 pounds	.....	4.28 lbs. TDN*
Cod liver oil, 1 pound	.....	1.14 lbs. TDN*
Salt, 0.05, pound	.....	
Finely ground limestone, 2.0	.....	
Total, 101.5 pounds	.....	76.47

\*Morrison's conversion Tables.

We assumed that 1 gm. TDN has an energy value of 4 Cal. (kilocalories), or 1 pound TDN is equivalent to 1814 Calories. By this assumption 1 gm. of this feed mix was computed to be equivalent to 3 Cal. TDN per gram, or 1360 Cal. TDN per pound of feed. All future computations in this paper will thus be made with reference to feed consumed, equivalent to 3 Cal. per gram or 1360 Cal. per pound of feed.

The energy value of eggs was found by analyzing a dozen No. 1 eggs, with the following results<sup>a</sup>:

Weight 1 dozen No. 1 eggs	.....	696.1 grams
Weight 1 dozen No. 1 eggs less shells	.....	610.1 grams
Weight 1 dozen No. 1 eggs shells	.....	86.1 grams
Weight 1 dozen No. 1 eggs less shells, dry	.....	159.4 grams
Weight 1 dozen No. 1 eggs shells only, dry	.....	65.4 grams

<sup>a</sup>We are indebted to Mr. Virgil Herring for these results.

So that

- 12.28% of whole "wet" egg is shell
- 68.27% of whole "wet" egg is water
- 74.46% of whole "wet" egg *less shell* is water
- 31.73% of whole "wet" egg is dry matter
- 25.54% of whole "wet" egg less shell, is dry matter.

Combustion value (by bomb calorimeter) of whole eggs. .1108.6 Cal.

Combustion value (by bomb calorimeter) of eggless shell 1088.6 Cal.

So that in terms of one egg of the dozen No. 1 eggs the

- Weight of the whole egg is .....58.01 grams
- Combustion value of a whole egg .....92.4 Cals.
- Combustion value of an egg less shell .....90.8 Cals.
- Combustion value of 1 gram dry whole egg ....4.987 Cals.
- Combustion value of 1 gram dry whole egg  
less shell .....6.987 Cals.

Combustion value of 1 gram whole ("wet") egg 1.6 Cals.

It may be noted that in dietetic practice it is customary to assume that the combustion value of a dozen eggs is 850 Calories, of course not including the shells, as contrasted to our result on No. 1, 58-gram, eggs of 1089 Cal. per dozen *not including shell*, and 1109 Calories including shells. We may also note for comparative purposes that 1 quart of milk containing 4% fat is equivalent to 750 Calories or 1 pound to 340 Calories, and that a pound of medium-priced fresh meat is equivalent to 700-1000 Calories; so that a dozen eggs, a pound of fairly fat meat,  $1\frac{1}{3}$  quarts of 4% milk have roughly the same caloric value. The actual values depend on the percentage of fat.

The average weight of the eggs laid by the birds under observation was not 58.01 grams as we found in the dozen of No. 1 eggs, but only 54.76 grams, and the average caloric value of such an egg is therefore not 92.4 Calories, but  $92.4 \times \frac{54.76}{58.01} = 87.2$ , the value used in the following computations.

Our data are unsatisfactory in several respects. The housing was very poor—too hot in the summer, too cold and drafty in the winter—with resulting unsatisfactory health and production of the birds. Of course, the lower the production level, the greater the maintenance cost per egg produced, and consequently the lower the gross or overall energetic efficiency. This situation explains in part the unusually low efficiency level of egg production of this group of birds. Nor were the feed records satisfactory. We have not learned how to keep the birds from losing some of the ground feed. Recently we have



developed a new feeding method which it is hoped will prevent feed loss and with which we shall repeat this work to obtain more rigorously quantitative food-consumption data.

### III. METHOD OF ANALYZING DATA

One of the objects of this paper is to "partition" the TDN consumed among the three major uses: egg production, maintenance, and gain (or loss) in live weight. For this purpose we shall use partition equation 7 previously defined:

$$\text{TDN} = A + B (\text{egg}) + C M^{0.73} + D \Delta M \quad (7)$$

Equation 7 is a statement of an energy balance between TDN consumption on the left side, and egg production, maintenance, and weight-gain on the right side. The significance of its parameters (B, C, D) depends on the accuracy of the basic data (TDN, egg, live weight, live-weight gains), the size and homogeneity of population, range of data, goodness of equation, and method of fitting equation to data.

We solved the equation by the method of least squares, which determines the values of B, C, and D so that the sum of the squares of the differences between observed TDN and TDN computed from equation 7 is a minimum. The solution consists in substituting in three "normal equations", and simultaneously weighting the trends of TDN with each of the other three variables (egg, M,  $\Delta M$ ) in equation 7 in such manner as to give a minimum value for the sum of the squares of the differences. The same result may be obtained by the following step-by-step procedure: Plot TDN successively against each of the independent variables, eggs,  $M^{0.73}$ , and  $\Delta M$ ; correct observed TDN values for the influence of one variable by approximating TDN cost per unit of that variable; subtract computed TDN required for the one variable from the observed TDN for each datum; correlate corrected TDN with another variable and determine a second correction. Thus are obtained the first approximations of the parameters. By continuing this process of approximation, the three trends (TDN vs egg; TDN vs  $M^{0.73}$ ; TDN vs  $\Delta M$ ) approach more and more closely to the ideal fit when the sum of the squares of the differences between observed TDN and computed TDN is a minimum. The use of the "normal equations" in the least squares method merely eliminates the laborious successive approximations.

An obvious objection is that equation 7 was formulated on the assumption that the egg secretion, maintenance, and weight-gain factors are independent. This is by no means certain. Moreover, since the coefficients in equation 7 are computed by the method of

least squares, it is clear that if the value of one coefficient is too high due to some experimental or biological situation, the values of the other coefficients will be influenced thereby. Each of the four terms represented in equation 7 has its separate set of experimental errors and biological variations. When combined into one interrelated system, each of these terms influences the value of every other term. There consequently results a very complex system of interinfluencing relationship.

A large population compensates and smoothes out individual experimental errors and biological variations so that there result dependable average values for the equation constants B, C, and D in equation 7. But if a small population is combined with large errors and variations, the equation constants are no longer dependable, often absurd.

Taking, by way of illustration, the data for the following 10 of 28-day random observation we obtain the following results:

Feed/Day gms.	TEN RANDOM OBSERVATIONS		Gain/Day (±) gms.
	Eggs/Day gms.	(Weight, gms.) <sup>0.73</sup>	
129.46	8.86	309.8	9.68
142.07	24.78	308.6	6.71
139.07	18.54	304.2	7.75
141.96	36.39	330.6	-3.75
111.64	6.00	358.7	1.43
129.46	0.00	305.9	10.75
101.18	17.25	280.2	1.32
130.18	11.82	304.4	15.89
117.71	23.86	314.2	-0.36
100.11	13.14	304.3	9.46

The partition equation used was

$$\text{Feed} = B (\text{eggs}) + C (\text{Weight})^{.73} + D (\text{Gain})$$

The summations for the above data are:

$\Sigma \text{Feed} = 1242.84$	$\Sigma (\text{Feed}) (\text{Eggs}) = 20,489.7210$
$\Sigma \text{Eggs} = 160.64$	$\Sigma (\text{Feed}) (\text{Weight}^{.73}) = 388,259.045$
$\Sigma \text{Weight}^{.73} = 3120.9$	$\Sigma (\text{Feed}) (\text{Gain}) = 7410.0280$
$\Sigma \text{Gain} = 58.88$	$\Sigma (\text{Eggs}) (\text{Weight})^{.73} = 50141.310$
$\Sigma (\text{Feed})^2 = 156,722.1452$	$\Sigma (\text{Eggs}) (\text{Gain}) = 594.1457$
$\Sigma (\text{Eggs})^2 = 3575.7458$	$\Sigma (\text{Weight}^{.73}) (\text{Gain}) = 17,961.082$
$\Sigma (\text{Weight}^{.73})^2 = 977,776.03$	$N = 10$
$\Sigma (\text{Gain})^2 = 674.3146$	

The proper summation values are substituted in the three normal equations:

$$B \Sigma (\text{Eggs})^2 + C \Sigma (\text{Eggs}) (\text{Weight}^{.73}) + D \Sigma (\text{Eggs}) (\text{Gain}) - \Sigma (\text{Feed}) (\text{Eggs}) = 0$$

$$B \Sigma (\text{Eggs}) (\text{Weight}^{.73}) + C \Sigma (\text{Weight}^{.73})^2 + D \Sigma (\text{Weight}^{.73}) (\text{Gain}) - \Sigma (\text{Feed}) (\text{Weight}^{.73}) = 0$$

$$B \Sigma (\text{Eggs}) (\text{Gain}) + C \Sigma (\text{Weight}^{.73}) (\text{Gain}) + D \Sigma (\text{Gain})^2 - \Sigma (\text{Feed}) (\text{Gain}) = 0$$

$$B \ 3575.7458 + C \ 50141.310 + D \ 594.1457 - 20,489.721 = 0$$

$$B \ 50141.310 + C \ 977776.03 + D \ 17961.082 - 388,259.045 = 0$$

$$B \ 594.1457 + C \ 17,961.082 + D \ 674.3146 - 7410.0280 = 0$$

Solving these equations we obtain  $B = 1.16$ ,  $C = .299$ , and  $D = 1.96$ , so that

$$\text{Feed} = 1.16 (\text{egg}) + .299 (\text{weight})^{0.73} + 1.96 (\text{gain})$$

The standard error of estimate of Feed,  $S_{\text{Feed}}$ , for equation 7, can be computed from the equation

$$S^2 = \frac{\Sigma (\text{Feed})^2 - [B \Sigma (\text{Feed}) (\text{Eggs}) + C \Sigma (\text{Feed}) (\text{Weight}^{.73}) + D \Sigma (\text{Feed}) (\text{Gain})]}{N - m}$$

where  $N - m$ , the number of degrees of freedom equals the number of observations less the number of arbitrary constants in the equation fitted; thus  $N - m = 10 - 3 = 7$ .

Substituting:

$$S^2_{\text{Feed}} = \frac{156722.1452 - (1.15633 \times 20489.721) - (.298769 \times 388259.045) - (1.96047 \times 7410.028)}{7}$$

$$S^2_{\text{Feed}} = \frac{156722.1452 - (23692.8790 + 115999.7666 + 14527.1376)}{7} = \frac{2502.3620}{7} = 357.48029$$

$$S_{\text{Feed}} = 18.91$$

The coefficient of multiple correlation of Feed with the combined effect of Eggs, Weight<sup>.73</sup>, and Gain can be computed as follows:

$$R^2 = \frac{[B \Sigma (\text{Feed}) (\text{Eggs}) + C \Sigma (\text{Feed}) (\text{Weight}^{.73}) + D \Sigma (\text{Feed}) (\text{Gain})] - \frac{(\Sigma \text{Feed})^2}{N}}{\Sigma (\text{Feed})^2 - \frac{(\Sigma \text{Feed})^2}{N}}$$

$$R^2 = \frac{154219.7832 - 154465.1265}{156722.1452 - 154,465.1265}$$

which gives an impossible result since  $R^2$  is negative.

Does this mean that equation 7 is wrong? Not necessarily. It means that the number of birds in the population is too small in comparison to the variability. The data points are too irregular and too few to give the equation a lead, so to speak, to the real situation. The data for the three sets of sign posts involved in showing the road (TDN trends for egg production, maintenance, weight gain) are so few, and distributed so erratically, that they are blurred and therefore useless as guides for reaching the desired goal.

It is not the scarcity of the data as much as the combination of scarcity, limited range, and erratic distribution of data that is responsible for the erratic results. The reliability of the equation parameters is conditioned by the accuracy of the data as well as by the number. To summarize, equation 7 gives dependable average values separately, for egg production, maintenance, and weight-gain, but only provided that the population is reasonably large and the data are reliable. The resulting fitted equation can not be used for

evaluating net efficiency of egg production of an individual bird because an individual bird's maintenance or weight-gain cost is likely to differ from the average, depending on her muscular activity, fatness, composition of the weight gains, etc. These properties of equation 7 must be kept in mind when interpreting its constants and net efficiency values listed in Table A (in the appendix).

As regards the relative significance and definiteness of gross and net efficiencies, gross efficiency, as indicated by equation 3, is clear cut. It is simply the ratio of energy in eggs produced to energy in TDN consumed (assuming 1 gm. TDN has an energy content of 4 Calories). No theoretical assumptions are involved in estimating gross efficiency if the weight-gain factor is ignored.

The meaning of net efficiency is, on the contrary, quite involved, as indicated by equation 6. The numerical value of net efficiency is dependent not only on the reliability of the basic data (egg energy produced, TDN energy consumed, gain or loss in live weight) but also on the goodness of partition equation employed, number of birds included in the computations, range in live weight and egg production, homogeneity with regard to relative inherited capacities for egg production, fattening, maintenance-need levels, etc.

Moreover, as indicated by the list of feed uses on page 7, the numerical value of net efficiency will depend on fine shades of definition. The statement that net efficiency represents the efficiency of the reproductive system as a machine apart from the rest of the body is true but not precise. Thus if the feed energy is expressed in terms of TDN, the net efficiency term includes the 20 to 30 per cent of energy loss incident to transforming TDN energy into Armsby's net energy.

This discussion is intended to make it clear that the term net efficiency of egg production as given in Table A has a special connotation. It is possible that if the TDN term in equation 7 were replaced by Armsby's net energy, the net efficiency would reach 90 or 95% instead of 70%; if other wastes incident to the transformations of nutrients as they enter the blood stream, into finished egg precursors, were deducted, then the net efficiency might reach still higher levels.

Practical poultry investigators may suggest that instead of evaluating TDN cost of maintenance from equation 7, one should determine TDN cost of maintenance by direct feeding trials on non-laying birds of various weights, and the TDN cost of egg production by the TDN consumed during laying above the determined maintenance TDN. In other words, evaluate TDN needs separately, for maintenance,

egg production and weight-gain by the customary feeding-trial method instead of the present mathematical partition method. The answer to this suggestion is that our theoretical method may be more practical than the suggested method for the reason that the mathematical method is less expensive and less difficult than the feeding-trial method. Otherwise the relation between body weight and food needs for maintenance would have been determined. We could not find any data on the relation between body weight and food needs for maintenance of non-laying mature fowls. As previously emphasized, we think it necessary to have many birds in order to compensate for variability in maintenance costs (some are "hard" keepers, others "light" keepers; some are fat, others thin; some have a high water percentage in their body, others low) and to furnish a wide range of live weight. Moreover, as indicated above, the maintenance cost of a laying hen is probably higher than of a non-laying hen of the same weight not only because of stimulating action of hormones etc., but also because the utilization of the TDN may be different at the higher nutritional level associated with ovulation. It is not possible to evaluate maintenance of a laying fowl from the maintenance expenditures of non-layers.

#### IV. RESULTS OF ANALYSIS OF ORIGINAL DATA

##### 1. Average and Maximum Efficiency of Egg Production

By way of introduction to the problem of comparative efficiency of productive processes in farm animals, we may quote the following well known values from Jordan's "The Feeding of Animals", 1901.

Animal and product	Edible solids per 100 pounds of digestible organic matter in the ration
Cow, milk	18.0
Hog, carcass	15.6
Calf, carcass	8.1
Fowl, egg	5.1
Fowl, carcass	4.2
Steer, carcass	2.8
Sheep, carcass	2.6

Jordan's ratio of edible solids per 100 pounds of digestible organic matter in the ration is very roughly equivalent to our percentage gross energetic efficiency. Jordan's 18% value for milk production may be considered as being near the 30% gross efficiency value we reported for milk production in "good" experiment station cows (see Missouri Agr. Exp. Sta. Res. Buls. 222, 238, and 239). Jordan

evidently believed that the efficiency of milk production is about 3½ times as great as of egg production. It is surprising that poultrymen have not heretofore challenged Jordan's low placement of egg production in the efficiency scale of agricultural productive processes, and the purpose of this bulletin is to reexamine this problem factually and critically especially in the light of our new data.

## 2. Data and Equation Inferences

Our data are summarized in Table A in the appendix and in Fig. 2. Table A includes among other information the value of the constants of equation (7) fitted to the data. The equation constants are seen to vary rather violently from month to month. Let us discuss equation (7) when fitted to represent all the data. The equation then becomes

$$\text{Feed} = 0.692 (\text{egg}) + 0.300 M^{0.73} + 1.07 \Delta M \quad (8)$$

which indicates that 0.692 gram feed was expended for producing 1 gram whole egg (including shell); 0.30 gram feed was expended to maintain one unit of  $M^{0.73}$  body weight; and 1.1 gram feed was expended for changing body weight by 1 gram. We assumed that the same amount (but of different sign) of feed was involved in gaining or losing unit body weight. This assumption is subject to criticism. However, since the fraction of the feed used for body weight changes is relatively insignificant, the assumption was perhaps justified in the interest of simplified computations.

## 3. Net Efficiency

Since 1 gram of feed was computed to be equivalent to 3 Calories of TDN in the feed, and since 1 gram whole egg was found to have a fuel value of 1.6 Calories, the *net* efficiency of egg production (not including maintenance and body-weight changes) is given by the equation

$$\begin{aligned} \text{Net energetic efficiency} &= \frac{\text{gm. egg} \times \text{Cal./gm}}{B \text{ gm. feed} \times \text{TDN Cal./gm feed}} = \frac{1 \times 1.16}{0.692 \times 3} \\ &= .77 \text{ or } 77\% \quad (8b) \end{aligned}$$

That is to say, out of 100 Cal. TDN consumed *above maintenance and above live weight changes* as computed by us, 77 Calories were recovered in the eggs, and the remainder expended for the cost of various intermediate and end transformations. It may be noted that the *net* efficiency of milk production in 243 experiment station cows was computed to be 62%. The difference between 62% and 77% in *net* efficiencies of milk and egg production appears to be

within the limits of variability of the data and equation constants\*.

The *net* efficiency is the same for egg as for milk production; this means that the energetic efficiency of transforming TDN into eggs when maintenance cost is not included is the same as the efficiency for milk production when maintenance cost is not included. This means that the *ovary and oviduct produce egg from egg precursors with the same energetic efficiency as the mammary gland produces milk from milk precursors.*

#### 4. Gross Efficiency

While the *net* efficiency (not including maintenance) is the same for egg and milk production, the overall or *gross* energetic efficiency of egg production including maintenance cost appears to be (Table A and Fig. 2) considerably below that of milk production. As previously noted, "ordinary" cows produced milk with an overall energetic efficiency of about 30%, and "extraordinary cows" may reach a maximum of about 47% (a 700-pound Jersey produced 26,000 pounds of 4% milk in one year had a computed efficiency of 47.5%). Table A (in the appendix) shows that the group of 55-egg birds under consideration produced the eggs (with respect to TDN) at a gross or overall energetic efficiency of about 10%; and Fig. 1 based on equation 8 shows that the theoretical maximum of gross efficiency of a 4-pound hen is of the order of 28%—which is considerably below the estimated 47% top energetic efficiency of milk production.

How shall we explain the result that while *net* efficiency appears to be the same for egg as for milk production, *gross* efficiency of egg production is very much below that for milk production? This seems to be a very important problem calling for detailed discussion.

Since the above data were obtained, additional data accumulated on New Hampshire Reds under more controlled and more favorable conditions. The results are shown in the following table.

Date of 28-day period	No. of birds	Av. Live Wt., gms.	Av. Daily Live Wt. Gain	Eggs per Bird	Average daily egg production			Ave. daily feed consumption		% Energetic Efficiency not corrected for weight gains
					gms./day	Cal./day	Per cent of possible production	gms./day	TDN Cal./day	
10/23/37 to 11/19/37	88	2282	4.8	10.3	20.0	32.0	36.3	112.0	336.0	9.5
11/20/37 to 12/17/37	73	2419	6.9	9.3	18.8	30.1	33.2	114.6	343.8	8.7
12/18/37 to 1/14/38	71	2544	1.6	15.5	33.6	53.8	55.4	129.9	389.7	13.8

\*Theoretically equation (7) and (8) should have an additional parameter constant A, thus:  

$$\text{TDN} = A + B (\text{egg}) + C M^{0.73} + D \Delta M \quad (9)$$
 Fitting equation (9) to the data by the method of least squares resulted in the equation  

$$\text{Feed} = 7.77 + 0.688 (\text{egg}) + 0.273 M^{0.73} + 1.09 \Delta M \quad (10)$$
 the constants of which do not differ substantially from those in equation 8. The standard error of estimate of equation 8 is 17.70 and of equation 10 is 17.71; the index of correlation of equation 8 is 0.722, and of equation 10 is 0.724, indicating that leaving out the parameter constant does not appreciably alter the situation.

## 5. Comparison of Energetic Efficiencies of Egg and Milk Production with Critical Discussion of Causative Mechanisms

We assumed that the *net* energetic efficiency of egg production does not depend on the number of eggs produced that is, it does not depend on the time factor; and we found on the basis of this assumption that the net efficiency that is, the efficiency of the ovary-oviduct system for converting egg precursors to eggs, is equal to the mammary system for converting milk precursors to milk.

The *gross or overall* efficiency on the other hand depends also on the amount of egg produced per year. The time factor is a vitally determining factor in the gross efficiency. It is obvious that the more egg produced per unit time, the smaller the overhead maintenance expense per unit egg, and consequently the higher the gross efficiency.

If we accept the above three statements that: (a) the *net* efficiency of egg or milk production is not appreciably dependent on the time factor or on the productive rate; (b) the *net* efficiency of egg production is the same as of milk production (that is, that the efficiency of the ovary-oviduct system for secreting egg is the same as of the mammary gland for secreting milk); (c) the *gross or overall* efficiency is sensitively dependent on the time factors or on the speed of egg or milk production, then the conclusion follows that the apparently lower *gross* energetic efficiency of egg production as compared to milk production is due to production rate differences in comparison to maintenance expense rates between fowls and cows; that is, the ratio  $\frac{\text{Egg Calories}}{\text{Maintenance}}$  is greater than the ratio  $\frac{\text{Milk Calories}}{\text{Maintenance}}$ .

**A. Comparison of energetic efficiencies of "ordinary" fowls, cows, and rats:** The above statement may be illustrated by section A, Table 1, comparing the ratios of milk-yield energy in dairy cattle<sup>9</sup> to their basal metabolism, and egg-yield energy in fowls<sup>10</sup> to their basal metabolism. (It is assumed that maintenance is the same multiple of basal metabolism in cows and fowls, an assumption which is by no means proved. It would be better to compare the energy yields to maintenance costs, but maintenance data are less available than basal metabolism data.) The basal metabolism was computed from the equation Basal Met. = 70.5 M<sup>0.73</sup>, the results of which are in good agreement with the recorded values in the literature.

Section A in Table 1 shows that *per unit of estimated basal metab-*

<sup>9</sup>Reported in Mo. Res. Bul. 238.

<sup>10</sup>S. C. W. Leghorns based on the Waite Maryland data, which will be presently discussed in detail.



TABLE 1.—COMPARISON OF EGG-CALORIE PRODUCTION IN DOMESTIC FOWLS, MILK-CALORIE SECRETION IN DAIRY COWS AND RATS WITH REGARD TO THE CORRESPONDING BASAL METABOLISM AND BODY WEIGHT

	A		C	B		
	"Ordinary" producers			"Extraordinary producers		
	Cows	Fowls	Rat	Champion Holstein Cow 1	Champion Jersey Cow 1	Champion Fowl 1
Number of individuals	368	478	1			
Body Wt., Kg.	513 (1130 lbs.)	1.7 (3.6 lbs.)	0.25	771 (1700 lbs.)	318 (700 lbs.)	1.8 (4 lbs.)
Estimated basal met. Cal./Day	6700	104	25	9000	4700	108
Production/Year	12200 lbs. 4% milk	201 Eggs	—	36476 lbs. 4% milk	26000 lbs. 4% milk	360 eggs
Production/Day	33.4 lbs. 4% milk	30.9 Eggs	70 Cal.	100 lbs. 4% milk	71 lbs. 4% milk	1 egg or 56 grams
Ratio Cal. basal met. to body weight Kg.	13	61	100	11.7	12.3	60
Calorie equivalent of daily production	11440	49.4	70	34000	24140	90
Ratio Calories in daily production to basal met. per day	1.7	0.48	2.6-2.8	3.8	5.1	0.83
Ratio Calories in product to Body Weight in Kg.	22	29	260	44	63	50
Estimated Energetic Efficiency with respect to TDN	31%	16%	—	43.5%	47.5%	27%

olism the "ordinary" cow produces about 3 times as much milk energy as the "ordinary" fowl produces egg energy.

But Table 1 also shows that *per unit body weight*, the average fowl produces more egg calories than the cow produces milk calories. The poultryman might be tempted to take this fact to mean that the fowl is relatively more productive than the cow; that the fowl is relatively more efficient than the cow; that the fowl's potentialities are relatively more developed than the cow's. The following discussion indicates some objections against such an interpretation.

We have demonstrated that *per unit body weight* small dairy cows produce more milk energy than large. This might be thought to indicate that small cows are more efficient than large. However, such is not the case because maintenance cost is likewise greater in small than large cows<sup>11</sup>, so that the two tend to compensate each other: the extra production per unit body weight in the small cow just covers the extra maintenance cost per unit weight in the small cow above the large. In fact it can be shown that *maintenance feed* per unit live weight tends to increase with decreasing size of animal in *such manner than energetic efficiency* (i.e., ratio of energy in milk to energy in feed) *tends to be independent of live weight*.

<sup>11</sup>Missouri Agr. Exp. Sta. Res. Bul. 220, 1934.

We have likewise shown (in Section C, Table 1) that *per unit body weight* a rat produces from 4 to 13 times more milk calories but is no more efficient energetically than a cow, because the maintenance cost *per unit body weight* in the rat is correspondingly greater (8 to 9 times) than in the cow.

In brief, body weight is not a good reference base for comparing productivities. Everyone is familiar with the fact that a 200-pound man does not produce at twice the speed, does not produce twice the work, and does not eat twice as much food as a 100-pound man. The only rigorous method for comparing production efficiencies is by means of the ratios  $\frac{\text{Calories in product}}{\text{TDN Calories consumed}}$ . When it is not possible to compute efficiency from this ratio, the most logical reference base for comparative purposes is maintenance cost. Unfortunately, little is known concerning the maintenance cost of a fowl or a cow. For the present therefore, the most logical procedure is to use basal metabolism (or the 0.73 power of weight) as the reference base, as shown in Table 1.

The comparison in Table 1 shows that the ratio of egg calories to basal metabolism calories is considerably below the ratio of milk calories to basal metabolism calories. This comparison between production and basal metabolism substantiates our efficiency computations based on the data in the Table A. It therefore seems safe to conclude tentatively that the given average cow is an energetically more efficient producer of milk calories than is the fowl of egg calories. This, as previously noted, appears to be not because of efficiency differences of the mammary gland and ovary-oviduct system, but because of a *low egg production in comparison to the overhead maintenance cost in fowls than of milk production in comparison to maintenance cost in cows*.

The comparison in Table 1 shows an energetic efficiency of about 16% in the Leghorn fowl producing about 200 eggs a year, and about 32% in the dairy cow producing about 13,000 pounds of 4% milk per year. Roughly speaking then, "good" dairy cows are energetically considered about twice as efficient in producing milk from TDN as are "good" fowls in producing eggs from TDN.

Let us turn from "good" fowls and "good" cows to extraordinary-producing fowls and cows.

**B. Comparison of energetic efficiencies of "extraordinary" fowls and cows:** Since hens in official egg laying contests have laid between 350 and 360 eggs, let us assume that an extraordinary hen may lay 360 eggs in one year. We may compare a 360 egg record with

the milk record of 36,476 pounds FCM (4% milk) produced by the 1700-pound Holstein champion cow Carnation Ormsby Butter King "Daisy", and 25,946 FCM produced by the 700-pound Jersey champion cow Stonehurst Patricia's Lily. The comparison is presented in Section B of Table 1.

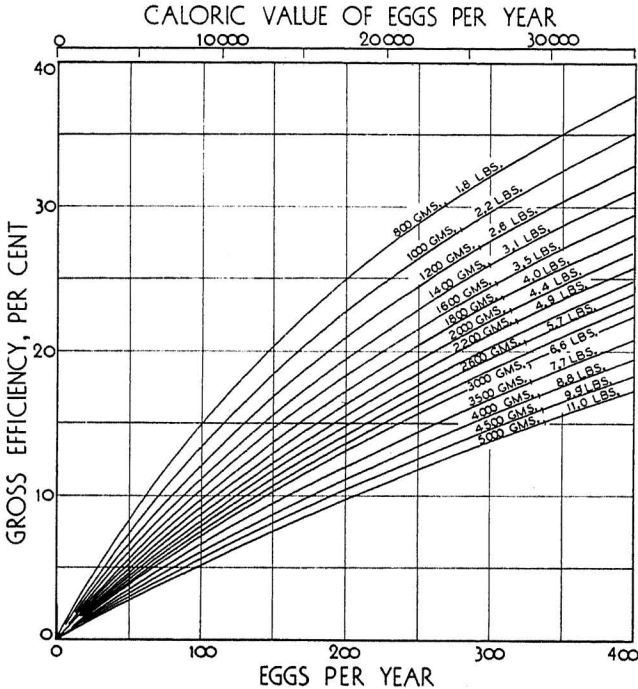


Fig. 1.—Gross efficiency of egg production as function of egg production level. Each curve is for a body weight (in grams) indicated on the chart. The curves are based on the equation (10),  $\text{Feed} = 7.77 + 0.688 (\text{egg}) + 0.273 M^{0.73}$  reduced to constant body weight and constant egg size (54.76 gm. per egg). One may legitimately question the propriety of extrapolating the poor production (60-75 eggs per year) of our birds to the 400-egg level, or the body weights (2000-2500 grams) of our birds to 800-5000 grams. The efficiency predictions given by these curves are frankly very speculative.

We estimated a 47.5% energetic efficiency of milk production for the Jersey, and 43.5% for the Holstein. For egg production, interpolation in Fig. 1, gives an energetic efficiency of 27% to a 360-egg fowl. The fowl's efficiency may also be estimated from the equation in Fig. 4,  $Y = 4.86 + 0.0577 X$ , in which Y is efficiency and X is egg production per year. By substituting egg number for X, the efficiency for 360 eggs is 25.6% and for 365 eggs is 25.9%. Clearly, the energetic efficiency of an extraordinary fowl is about  $\frac{1}{2}$  that of the champion cows and more nearly that of ordinary cows.

The second row from the bottom in Table 1 shows that the ratio of calories in product to *body weight* is higher in the extraordinary fowl than in the Holstein cow, but lower than in the Jersey cow. In general, on a per unit body weight basis champion cows are not superior to fowls.

But now consider the ratio of calories in product to estimated basal metabolism. This is less than 1 in the champion fowl, over 5 in the champion Jersey cow and nearly 4 in the champion Holstein cow. If we admit the validity of equations 8 and 8b and if we assume that maintenance cost is directly proportional to basal metabolism regardless of size or species (cow or fowl) we are forced to conclude that the higher overall efficiency of the cow than of the fowl is due not so much to differences between the energetic efficiency of the mammary gland to produce milk and ovary-oviduct to produce eggs, *as to higher milk-calorie production in comparison to maintenance cost in cow than of egg-calorie production to maintenance cost in fowl.*

**C. Physiologic significance of efficiency differences between egg and milk production:** The evolutionary and physiologic interpretation of these results is not simple.

While eggs and milk have analogous nutritive functions there are also differences. Joseph Needham aptly described the egg as a "closed box" or "cleidoic" system. A sharply limited amount of nutriment is locked up in the box as endowment for the young. The milk produced is on the other hand not sharply limited. The amount of milk produced per day is within limits responsive to need. A rapidly growing calf stimulates the cow to produce more milk than a slowly growing one. Likewise there is adjustment of production to twins or triplets. Moreover, vigorous rapid growth undoubtedly has survival value, so that there might have been an evolutionary tendency to greater milk production. On the other hand, there is a very definite limit to the number of eggs a hen can incubate, so that there might not have been the same evolutionary tendency for increasing egg as milk production. Evolutionary trends may have thus favored the development of various enabling mechanisms for relatively greater (relative to maintenance cost) milk than egg production. But then, neither is the production limit in the bird fixed, because if the eggs are removed from the nest of a wild bird, more eggs are usually produced to replace the lost eggs.

The situation appears different when viewed from the standpoint of production-energy cost. Two aspects have to be considered: (a) relative organizational complexity and consequently relative organiza-

tional energy expense; (b) relative time required for elaborating unit energy in product, and consequently relative overhead maintenance costs for the time required to make the products.

(a) *The complexity aspect:* The mammal might be said to dump her relatively homogeneous milk product into a cistern to be tapped at the will of the infant. The bird on the other hand packages her egg product most elaborately with inner shell membrane; outer shell membrane; shell; cuticle. The shell, composed mostly of  $\text{CaCO}_3$  (93-98%), has practically no energy value when analyzed calorimetrically, yet, of course, a great deal of "work" must go into its construction.

We have emphasized in the introduction the basic difficulty in evaluating the energetic efficiency of constructional processes because the organizational features are destroyed prior to reaching the calorimetric assay stage.

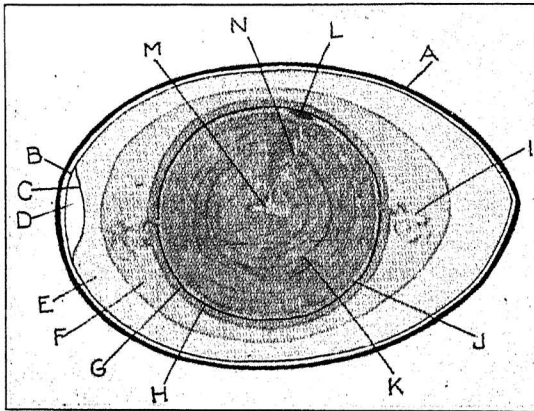


Fig. A (From E. W. Benjamin, Cornell Ag. Exp. Sta. Bul. 353, 1914).—Structure of the egg. A, shell; B, outer shell membrane; C, inner shell membrane; D, air cell; E, outer thin portion of albumen; F, middle jelly-like portion of albumen; G, inner dense portion of albumen; H, vitelline membrane; I, chalaza; J, thin film of white yolk inside of vitelline membrane; K, layers of yellow yolk separated by thin layers of white yolk; L, germinal disk; M, central part of yolk filled with white yolk; N, slender tube connecting center of yolk with region of germinal disk. Each of these structures is in turn made up of smaller structures, as for example, the shell is composed of: (a) gelatinous outer coating; (b) outer porous layer; (c) middle granular layer; (d) inner crystalline layer; (e) inner face layer, each of different structure. The inner shell membrane is a fine cellular structure bound by many intertwining fibres; the outer shell membrane, coarser in structure than the inner, is also composed of fibers, and so on.

Nor are the albumen and yolk parts of the egg homogeneous in the sense that milk is. It may be profitable to recall<sup>12</sup> some egg structures, illustrated in part by Fig. A.

Biologically speaking, the most important part of the egg is the germ, spoken of as the germinal disk when not fertilized and blastoderm when fertilized. The germinal disk develops into the embryo. The germinal disk, and its nutrient yolk, are wrapped together in the vitelline membrane. The yolk is made up of a series of concentric dark and light layers. The dark yolk is in turn made up of structural units ranging in size from 0.025 to 0.100 mm. in diameter, and the light yolk of units up to 0.07 mm.

The albumen is also made up of several layers. Closely adhering to the vitelline membrane is the dense chalaziferous layer connected with the chalazae. This layer is surrounded by the "dense white" layer which comprises 40 to 60% of total egg weight. This layer is a fibrous mesh work filled with thin albumen. Surrounding this fibrous layer is a more liquid mucilaginous albumen layer.

There is no doubt that there are many other structural complexities which await description. The important fact is that eggs have a more complex organization than milk, and that the energy expended for the organization is not included in the calorimetric measurements of energy content in the egg.

(b) *The time factor*: Interrelated with and paralleling the greater organizational complexity of eggs as compared to milk there is an absolutely and relatively greater time interval involved in producing an egg than in producing milk. It takes less time—to resort to a crude analogy—to produce a load of lumber than to produce a lumber house although the energy content may be the same in the two. If the time factor with its overhead expense is overlooked, then the energetic efficiency (net efficiency) of producing a load of lumber and house is the same. But if the time factor with its associated overhead *maintenance cost* is considered, then, of course, the ratio of energy in the lumber to the total energy expended in the entire period is less for the finished house than for the lumber. So as regards egg and milk production. If it is admitted that the egg is structurally more complex than milk, involving a longer biologic time interval in egg than milk production, then the difference between the energetic efficiencies of egg and milk production becomes obvious.

The time factor for the production of the albumen and shell in

<sup>12</sup>Cf. Lillie, F. R., *The development of the chick*, New York, 1919; Lippincott, W. A., revised by Card, L. E., *Poultry Production*, Philadelphia, 1934; Jull, M. A., *Poultry Breeding*, New York, 1932.

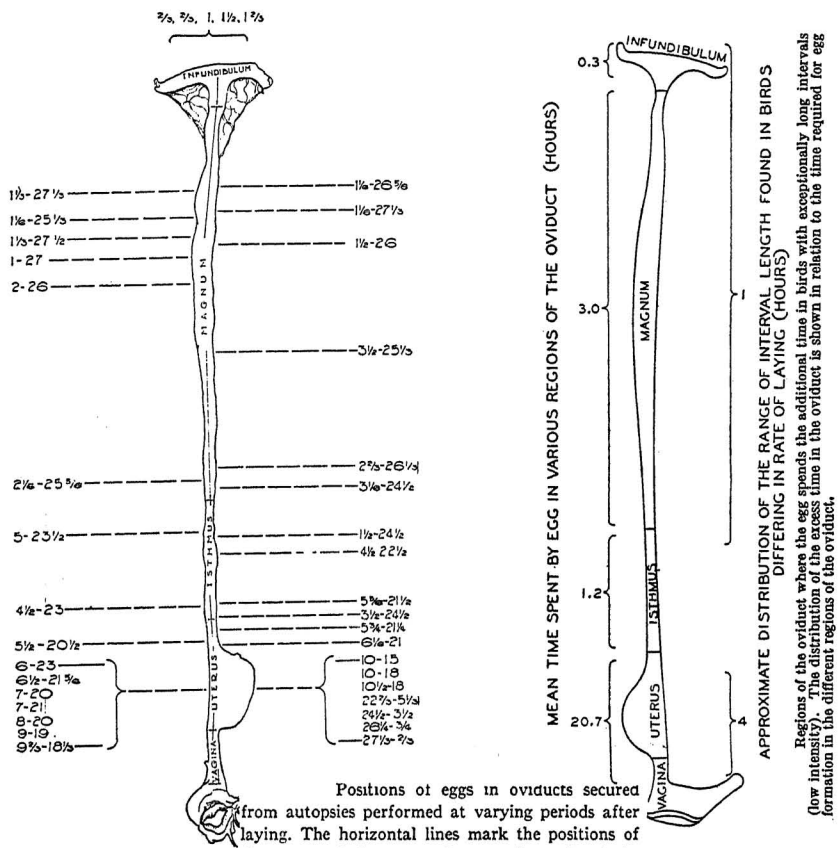


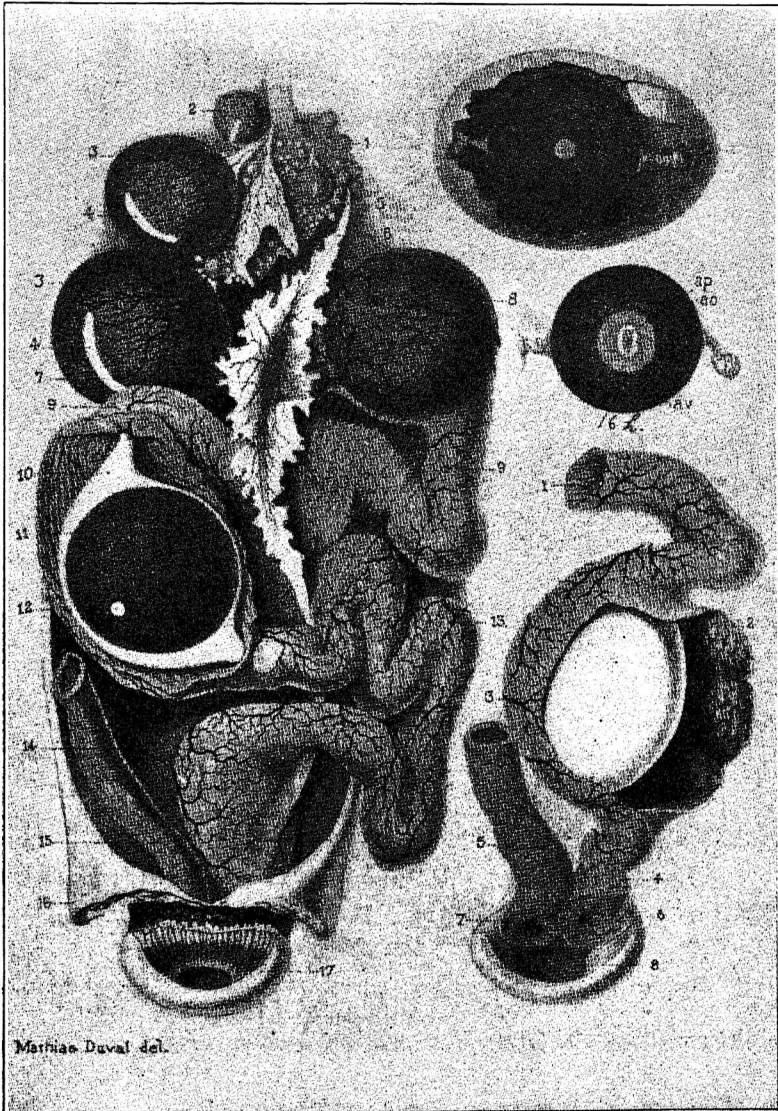
Fig. B.—The time relations of migration of the egg through the oviduct. (Courtesy of D. C. Warren.)

the fowl's egg has been worked out by Warren and Scott with considerable accuracy<sup>13</sup>. Fig. B, from Warren and Scott, illustrates the situation beautifully.

The "true egg" that is the germinal disk and yolk are formed in the ovary, and the surrounding envelopes of albumen, shell membranes, and shell are formed in the oviduct. The results of Warren and Scott are concerned with the time relations in the oviduct.

<sup>13</sup>Warren, D. C., and Scott, H. M., The time factor in egg formation, *Poultry Science*, 14, 195, 1935; physiological factors influencing the rate of egg formation in the domestic hen, *J. Agr. Res.* 51, 565, 1935. See also Pearl, R., and Curtis, M. R., Data regarding the physiology of the oviduct, *J. Exp. Zool.* 12, 99, 1912.





FROM DUVAL'S ATLAS

*Oviduct of a laying hen:* 1, ovary, with minute ovules; 2-3, yolk sacs; 4, suture line; 5, empty yolk sac; 7, funnel opening into oviduct; 8, yolk in oviduct; 9, albumen-secreting region; 10, albumen being secreted; 11, yolk passing through oviduct; 12, germinal disk; 13, isthmus; 14, uterus; 15, large intestine; 17, cloaca. On the right-hand side of the figure are shown, from the top downward: complete egg; yolk of egg incubated for sixteen hours; completed egg in uterus—(1) isthmus, (2) glands of uterus, (3) complete egg, (4) vagina, (8) cloaca

Fig. C.—The migration of the egg in the ovary and oviduct as pictured by Mathias Duval (1889), from Benjamin (l. c.).



When the yolk is fully formed, the follicle housing it ruptures, and the germinal disk and yolk system escapes into the infundibulum or funnel of the oviduct. Fertilization occurs in the infundibulum, and within about half hour of its arrival it departs for a journey of about 25 hours travelling slowly through the magnum (about 3 hours), isthmus (about  $1\frac{1}{2}$  hours), uterus (about 20 hours), vagina (about  $\frac{1}{2}$  hour). Most of the albumen, including the chalazae, is secreted in a period of about 3 hours in the albumen portion of the oviduct, and the remaining in the isthmus and uterus sections. The membranes are formed in the isthmus, and the shell in the uterus.

But the time factor in the formation of albumen and shell in the oviduct is only one, perhaps a relatively small, part of the total time involved in the formation of an egg. Little is known about the time relation of yolk and germinal disk formation<sup>14</sup>. The speed of egg production—and consequently its *gross* energetic efficiency—may not be limited by the speed of migration in the oviduct but by the speed of maturation of the ova in the ovary.

The mystery for the difference in energetic efficiency of egg and milk production clears up when the following facts are remembered: (1) egg and milk production are processes in *time*; (2) the flow of biologic time is inseparable from energy expenditure for overhead maintenance of the organism; (3) biologic organization-energy can not now be measured by physical (calorimetric) methods; (4) the egg is structurally more complex and requires more biologic time for its formation than milk. It is self evident that the more complicated the structure, and consequently the longer the time taken to construct it, the more energy expended for its construction and the less the gross energetic efficiency of the process when, as in the present case, the energy that goes into constructional work, cannot be recovered.

There is another aspect that might be mentioned, and that is the fact that in comparison to milk, egg is very rich in fat (64% of the total calories in egg, 49% of total calories in cow's milk), and that there is an energy expense in producing fat from carbohydrates. Egg is also richer in protein than is milk (35% of the total calories in egg, 21% of the total calories in cow's milk). Sugar, the least expensive physiologically to produce, is 21% of the total calories in cow's milk, and less than 1% in egg.

From a practical point of view, the lower energetic efficiency of

<sup>14</sup>See Rogers, C. A., Feeding color—an aid in studying physiological development, Proc. Intern. Assn. Instructors and Investigators in Poultry Husbandry, Vol. 1, p. 77, Ithaca, N. Y., 1912, and the following work, for attempts to investigate the time factor by feeding and injecting dyes.

egg production as compared to milk production is very interesting, but not important. The energy content of the egg is not the sole reason for its use. The egg, for example, is rich in all blood-forming elements while milk is not. Our present interest is in the factual and theoretical, interpretive, aspects.

From the theoretical viewpoint one might ask whether the possession of two reproductive systems, as sometimes happens<sup>15</sup>, would appreciably accelerate the process of total egg production, thereby decrease the overhead maintenance cost and raise the gross energetic efficiency more closely to the theoretical limit of net efficiency. It is, on the other hand, possible—indeed probable—that the rate of egg production is not limited by the capacity of the reproductive system but by the metabolic systems (circulatory, respiratory, excretory, digestive, assimilatory), in which case selection for “vitality” is more important than attempts to supplement the reproductive system directly either by selection for two reproductive systems or by hormonal treatment.

### 6. Body Weight vs. Efficiency

The problem of body weight vs. efficiency was already outlined in connection with Table 1 comparing the energetic efficiencies of fowls as egg producers, and rats and cows as milk producers. All other conditions (particularly degree of fatness and hereditary level of egg production) being the same, is a small or large fowl likely to be the more energetically efficient egg producer? The maintenance cost is the key to the answer. The efficiency will increase, decrease, or remain constant with increasing body weight if the ratio

$\frac{\text{Egg production}}{\text{Maintenance cost}}$  respectively increases, decreases, or remains constant with increasing body weight.

In equations (7), (8), and (9) we assumed that maintenance cost increases with the 0.73 power of body weight<sup>16</sup>. The answer to the question concerning the influence of body weight on efficiency of egg production must depend on the question whether both maintenance cost and egg production increase with the same power of body weight. Does maintenance cost increase with the 0.73 power of body weight? Does egg production increase with the 0.73 power of body weight? One purpose of collecting the data in Table A is to answer these questions.

<sup>15</sup>Cf. Atwood, H. and Snyder, H., A hen with two ovaries, *Poultry Sc.*, 2, 1922-3, 59; Crew, F. A. E., Paired oviducts in the fowl, *J. Anat.* 66, Part 1, 1931, 100.

<sup>16</sup>This assumption is based on the fact, reported in *Missouri Agr. Exp. Sta. Res. Buls.* 166 (page 93, 1932) and 220 (1934), that basal metabolism of mature animals of different species increases with the 0.73 power of body weight. This 0.73 power generalization may or may not hold for basal metabolism of animals of differing weights of the same species, or for maintenance cost.

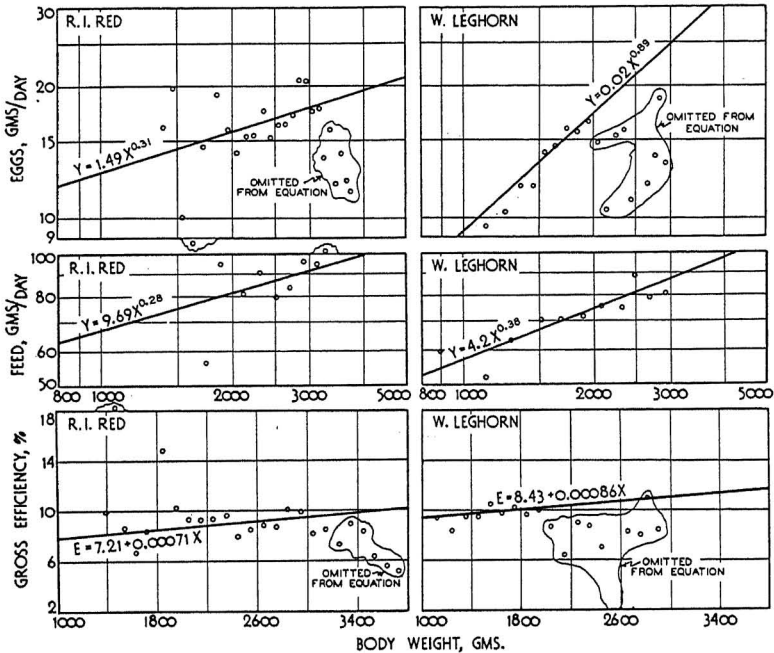


Fig. 2.—Influence of body weight on egg (grams) production, maintenance, feed consumption (non-laying hens), and gross efficiency of egg production.

Unfortunately, as shown in Fig. 2, the data in Table A are too erratic to give satisfactory answers to these questions. A part of this erratic distribution is due to the well-known fact that egg production declines after reaching a characteristic body weight (see Fig. 8). For this reason, the equations in Fig. 2 were fitted not to all the data, but only up to the body weight when egg production is maximum.

Preceding this body weight of maximum production, the egg production is seen, in the upper charts of Fig. 2, to increase not with the anticipated 0.73 power, but with the 0.31 power in the R. I. Reds, and with the 0.89 power in the W. Leghorns—a very inconclusive answer to the question “*how does egg production vary with increasing body weight?*”

As indicated by the middle chart in Fig. 2, there is similar uncertainty concerning the question, “*how does maintenance vary with increasing body weight in non-laying fowls?*” The data in Fig. 2, were obtained as follows: The records were kept by 28-day periods. Such of the 28-day periods during which no eggs were produced, and during which the fowls did not change body weight by over 2½

grams per day, were segregated, and equations fitted to them by the method of least squares. The data are shown below.

## WHITE LEGHORNS

Number 28-day periods	Av. Body Weight gms.	Av. Feed Consumed per day	Number 28-day periods	Av. Body Weight gms.	Av. Feed Consumed per day
1	886	59.8	2	1743	56.3
7	1127	51.8	8	1885	94.8
22	1298	62.6	5	2112	80.9
24	1517	70.0	7	2304	91.7
27	1688	70.1	12	2504	79.5
35	1890	71.5	11	2705	83.3
20	2080	75.3	13	2907	96.4
14	2311	74.5	2	3127	94.8
2	2491	88.1	4	3259	101.8
1	2686	78.0			
1	2930	80.8			

The equations fitted to these data (see Fig. 2) show that the feed consumption increased not with the 0.73, but with the 0.28 power in the R. I. Reds, and 0.38 power in the W. Leghorns, a completely unexpected result. Fig. 3 represents the relation between feed consumption and body weight when the data of both breeds were combined. Fig. 3 shows that when the non-laying periods of both breeds

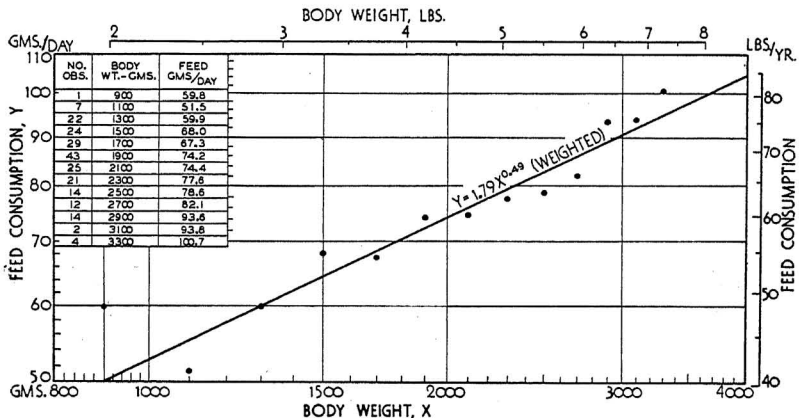


Fig. 3.—The feed consumption of the birds during non-laying 28-day periods increased with roughly the 0.5 power of body weight; i. e., increasing body weight by 100% increased feed consumption by about 50%.

are combined, the feed consumption tends to vary not with the 0.73 power as we assumed, but with the  $\frac{1}{2}$  power of body weight. That is, increasing body weight by 100% increases maintenance-feed consumption by about 50%.

Since Figs. 2 and 3 show that egg production increases at a greater rate than maintenance in non-laying fowls, one would expect that gross efficiency would increase with increasing body weight. This appears to be confirmed by the lower curves in Fig. 2—that is prior to body weight of maximum production. However, in view of the defects

and erratic distribution of the data, we do not consider this result as indicating the real situation. Indeed, we believe that gross efficiency of egg production is independent of body weight; that is, that (prior to body weight of maximum egg production) both maintenance cost and egg production increase at the same rate with increasing body weight, as will be shown in part in the following section.

## V. ANALYSIS OF PUBLISHED DATA

The value of this bulletin may be increased by computing gross efficiency of egg production from published data on egg production and food consumption. As the published data were secured for other purposes than efficiency computations, they lack certain details which we shall have to assume. In these computations we shall assume that 1 gram whole egg is equivalent to 1.6 Calories, and 1 gram chicken feed 3 Calories TDN per gram, or 1360 Calories TDN per pound.

### 1. Efficiency Levels

We may first cite the well-known paper by Byerly, Titus and Ellis on production and hatchability of eggs as affected by different kinds and quantities of proteins in the diet (*J. Agr. Res.* 46, 1, 1933). Their data are listed in columns 1 to 4 of the following Table 2, to which we appended column 5 giving the computed gross energetic efficiency of the egg production. Column 5 in Table 2 indicates that the gross energetic efficiency of egg production of 200-egg producers—a very high level—is only about 14 per cent. Some of the food, however, was used for growth, for which no correction was made.

TABLE 2.

Diet No.	Egg produced per gram of feed eaten after average date of 1st egg	Egg/hen per Pullet Year	Change in Body Weight gms.	Gross Energetic Efficiency* (not corrected for change in body weight)
1	0.229	197.0	316	12.2
2	0.212	187.5	252	11.3
3	0.231	188.1	341	12.3
4	0.205	168.0	358	10.9
5	0.172	145.8	-15	9.2
6	0.219	173.0	296	11.7
7	0.191	159.5	81	10.2
8	0.251	204.5	365	13.4
9	0.198	157.8	—	10.6

\*Column 5 was computed on the assumption that 1 gm. feed is equivalent to 3 Cal., and 1 gm. egg to 1.6 Cal. Thus  $\frac{0.229 \times 1.6 \times 100}{1 \times 3} = 12.2\%$ . The data are based on a 344-day period (Sept. 1929 to Aug. 1930).

Byron Alder (*Utah Agr. Exp. Sta. Bul.* 248, 1934) presented valuable material in his summary of seven Utah Egg-laying contests (November 1924—October 1931). We computed the gross efficiency from the average data on feed consumption and egg production with the results shown in Table 3.

TABLE 3.—ESTIMATED GROSS ENERGETIC EFFICIENCY OF EGG PRODUCTION OF THE UTAH EGG-LAYING CONTESTS, S. C. WHITE LEGHORNS.

Month	Grain lbs./ month	Mash lbs./ month	Total lbs./ month	Feed Calories per month	No. eggs per month	Egg Calories per month	Overall Energetic Efficiency
November	3.54	2.45	5.99	8158	13.8	1148	14.1
December	3.73	2.29	6.02	8199	13.5	1123	13.7
January	3.88	2.35	6.23	8485	15.4	1281	15.1
February	3.51	2.54	6.05	8240	17.4	1448	17.6
March	3.99	3.09	7.08	9643	20.8	1731	18.0
April	3.73	3.27	7.00	9534	20.1	1672	17.5
May	4. 4.02	3.11	7.13	9711	22.0	1830	18.8
June	3. 3.83	2.76	6.59	8976	20.6	1714	19.1
July	3.69	2.89	6.58	8962	19.7	1639	18.3
August	3.52	2.27	5.79	7886	17.6	1464	18.6
September	3.50	1.90	5.40	7355	15.3	1273	17.3
October	3.14	1.38	4.52	6156	11.7	973	15.8
Total/yr.	44.1	30.1	74.4	101305	207.9	17296	(Avg.) 17.0
Column	1	2	3	4	5	6	7

We computed Columns 3, 4, 6, and 7.

Table 3 indicates that the overall energetic efficiency of the Utah Leghorns is of the order of 17% on yearly basis, and 19% for the highest production period (May-June). These 19% efficiency birds may be considered to be fairly high producing fowls comparable to the high producing cows for which we found an overall percentage efficiency of 30%. The 10% difference in efficiency between cows and fowls may of course, be due to some errors in the data, or/and to erroneous assumptions in the computations. In view of the uncertainty of the results, it seems desirable to examine additional data in the literature that may throw further light on this problem.

TABLE 4.—ESTIMATED GROSS ENERGETIC EFFICIENCY OF EGG PRODUCTION OF THE MARYLAND EGG-LAYING CONTEST.

Breed	No. birds as No. "hen years"	Egg Production per year	Feed Con- sumption per year lbs.	Pounds Feed Consumed/ doz. eggs	Gross Ener- getic effi- ciency of egg production
S. C. W. Leghorns	4781.2	201.1	80.5	4.8	16.5
R. C. Brown Leghorns	10.5	148.0	61.3	5.0	15.9
Ancona	57.1	162.0	73.4	5.4	14.5
Black Leghorns	11.4	144.6	66.0	5.5	14.4
Barred Plymouth Rocks	459.0	188.3	88.7	5.7	14.0
White Plymouth Rocks	49.4	146.1	83.7	5.7	11.5
Australorp	21.7	180.2	88.4	5.9	13.4
R. I. Red	655.6	181.0	92.2	6.1	12.9
S. C. Buff Leghorns	10.7	121.8	63.8	6.3	12.6
Lamona	9.7	137.4	74.4	6.5	12.2
Dominique	90.2	134.0	74.6	6.7	11.8
Silver L. Wyandotte	11.5	151.9	84.7	6.7	11.3
S. C. R. I. White	33.0	149.4	84.6	6.8	11.6
Andalusian	21.1	139.6	79.8	6.9	11.5
Wt. Wyandotte	42.9	138.9	81.0	7.0	11.3
S. C. W. Minorca	10.4	127.4	80.5	7.6	10.4
Buff P. Rock	10.7	116.3	78.4	8.1	9.8
Mottled Brahma	10.9	113.2	77.2	8.2	9.7
Black Langshan	10.2	113.3	85.5	9.1	8.7
Jersey Black Giant	9.0	93.3	84.0	10.8	7.3

Notes: In Waite's bulletin the feed values are carried to three decimals, which we abbreviated to one decimal; the egg production is carried in the bulletin to two decimal places which we abbreviated to one place. No egg weights were given. The eggs were assumed to weigh 56 grams.

$$\text{Efficiency} = \frac{\text{egg gms.} \times 1.6}{\text{Feed lbs.} \times 1360}$$

R. H. Waite presented (Maryland Agr. Exp. Sta. Bul. 359, 1934) summaries of the results of six Maryland Egg-Laying contests (November 1925—October 1931) in very suggestive forms. Table 4 presents a summary of the Waite combined data. Unfortunately the egg weights are not given, so that for computing efficiency we had to assume egg weights. We assumed that the eggs weighed 56 grams each. This of course is not strictly true—the egg weights probably ranged from less than 50 to over 60 grams. Table 4 shows that, under these assumptions, the estimated gross energetic efficiency of Leghorns as egg producers is not far from 16 per cent.

These three sets of cited data substantiate Jordan's belief that the gross efficiency of egg production tends to be below milk production; however, the resulting efficiency values are considerably higher—perhaps 300% to 400% higher—than might be inferred from Jordan's figures.

It is evident from the cited data, and from *a priori* considerations, that the higher the production level the higher the overall energetic efficiency of egg production. This is shown graphically in Fig. 1 based on equation 8. Waite's summaries of the egg production and feed consumption of the Maryland Egg-Laying contests offer an opportunity of investigating this problem in greater detail.

## 2. Influence of Production Level on Gross Energetic Efficiency of Egg Production

Fig. 1, based on our data generalized by equation 8, represents the functional relation between gross efficiency of egg production and the production level. From Fig. 1 it appears that the maximum efficiency, attained on perhaps 300-egg birds, should be of the order of 25%. Does efficiency of egg production actually reach this level? By way of orientation, it is profitable to examine Waite's Maryland egg-laying contest data on egg production and feed consumption of birds in different production classes. As the egg weights are not given in Waite's report we assumed a constant egg weight of 56 grams. The energetic efficiencies of egg production thus estimated of three breeds are listed in Tables 5a, 5b, and 5c, and charted in Fig. 4.

Tables 5a to 5c and Fig. 4 show that the yearly range in gross efficiency of egg production in pens of "good" birds—good enough to be included in the given egg-laying contest—is, roughly from 10 per cent to 20 per cent. If a *pen* of birds can produce eggs at 20% it is probable that *individual* birds may reach much higher levels, perhaps 25% or even 30%. (We may note again that a good herd

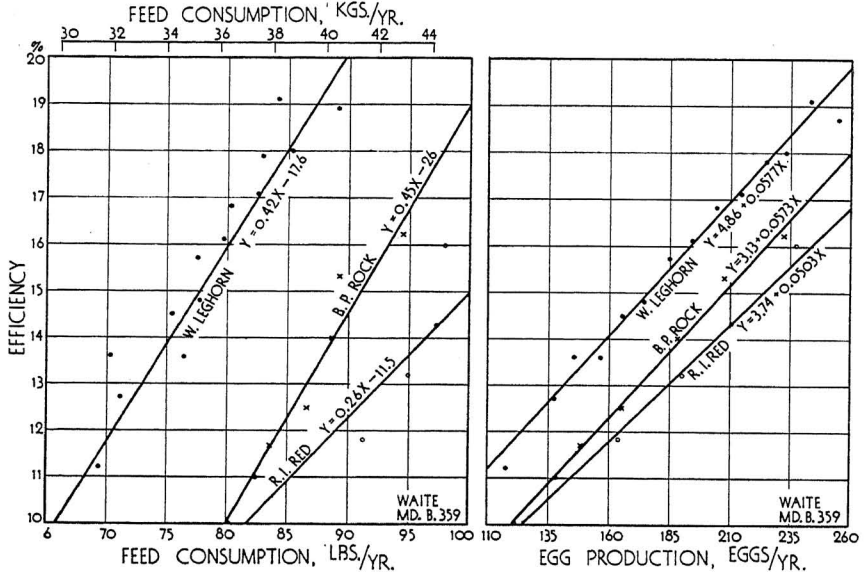


Fig. 4.—Gross or overall energetic efficiency of egg production as function of egg-production level based on Waite's Maryland-competition data. Compare with Fig. 1. Theoretically, the distribution cannot be linear, but it practically is, and so we fitted linear equations. The eggs were assumed to weigh 56 grams in all cases, which may explain in part the apparent differences in efficiency between the three breeds at a given egg-production number. Note the parallelism with the curve relating efficiency with feed consumption.

TABLE 5a.—EFFICIENCY OF EGG PRODUCTION IN *White Leghorns* AS FUNCTION OF PRODUCTION LEVEL.

Production Level eggs per year	No. birds (hen years)	Av. Weight per bird lbs.	Feed Consumed Per Bird lbs./year	Feed Consumed Per Doz. Eggs lbs.	Energetic Efficiency Per Cent
117.7	8.2	3.61	69.30	7.06	11.2
137.3	10.1	3.40	71.10	6.21	12.7
145.1	63.3	3.21	70.28	5.81	13.6
156.5	133.4	3.60	76.04	5.83	13.6
165.5	124.0	3.54	75.40	5.47	14.5
174.6	301.4	3.55	77.90	5.35	14.8
185.0	247.1	3.57	77.53	5.03	15.7
194.3	345.7	3.49	79.70	4.92	16.1
204.5	326.5	3.56	80.25	4.71	16.8
214.8	203.8	3.58	82.53	4.61	17.1
225.0	272.3	3.62	82.98	4.43	17.8
233.2	770.1	3.76	85.32	4.39	18.0
243.0	105.9	3.77	84.02	4.15	19.1
255.8	11.4	3.81	89.15	4.18	18.9

TABLE 5b.—EFFICIENCY OF EGG PRODUCTION IN *Rhode Island Reds* AS FUNCTION OF PRODUCTION LEVEL.

Production Level Eggs per Year	No. birds (hen years)	Feed Consumed per Bird pounds/year	Feed Consumed per dozen eggs pounds	Gross Energetic Efficiency %
121.4	29.9	80.3	7.94	10.0
138.1	71.7	82.5	7.16	11.0
163.9	127.5	91.4	6.69	11.8
190.2	175.0	95.0	5.99	13.2
210.7	133.4	97.2	5.53	14.3
237.6	66.5	97.9	4.95	16.0



TABLE 5c.—EFFICIENCY OF EGG PRODUCTION IN *Barred Plymouth Rocks* AS FUNCTION OF PRODUCTION LEVEL.

Production Level Eggs per Year	No. birds (hen years)	Feed Consumed per Bird pounds/year	Feed Consumed per dozen eggs pounds	Gross Energetic Efficiency %
148.4	10.4	83.6	6.76	11.7
165.2	139.0	86.7	6.80	12.5
188.4	161.7	88.7	5.65	14.0
207.7	79.7	89.3	5.16	15.3
232.8	57.3	94.5	4.87	16.2

of cows was shown to produce milk with an efficiency of 30%, and a great individual cow was estimated to produce milk at 47% efficiency.)

### 3. Influence of Body Weight on Production Level and Gross Efficiency

It is evident enough that of two birds of unequal size—say a 3-pound Leghorn and 6-pound R. I. Red—producing the same number of eggs of the same weight the smaller Leghorn will produce the eggs at a higher energetic efficiency than the large R. I. Red; because the 3-pound bird needs less food for maintenance than the 6-pound. This may explain the higher efficiency of the Leghorn as compared to the heavier breeds. Thus from Table 5a, 233-egg, 3.76 pound Leghorns are recorded to produce at an efficiency of 18%; from Table 5c 233-egg, 5.5-pound B. P. Rocks produced at 16% efficiency. However, it is possible that this recorded difference in efficiency between heavy and light birds producing the same number of eggs is not real; it is possible that the heavier birds compensate for their greater maintenance cost by laying larger eggs, containing more energy per egg than smaller birds. This is a reasonable assumption. For purposes of computing the efficiency of egg production in large and small birds in Table 5 we were forced to assume the same egg weight (56 grams) for all birds, because the egg weights were not recorded.

a. **Egg weight vs. body weight:** There appears to be no generalization in the literature giving a quantitative relation between egg weights and body weights of fowls. In Fig. 5 we plotted egg weights against body weights reported by A. G. Taylor for the 9th and 10th Annual Canadian National Egg Laying Contests (Dominion of Canada, Department of Agriculture, Bulletin 139, new series, Ottawa, 1930). From Fig. 5 it appears that for a given body weight the Leghorn lays heavier eggs than the R. I. Red; and the R. I. Reds lay heavier eggs than white Wyandottes; and the latter heavier than B. P. Rocks. Thus for body weight 5 pounds, the weight per dozen eggs is seen to be for Leghorns a little over 25 ounces; for R. I.

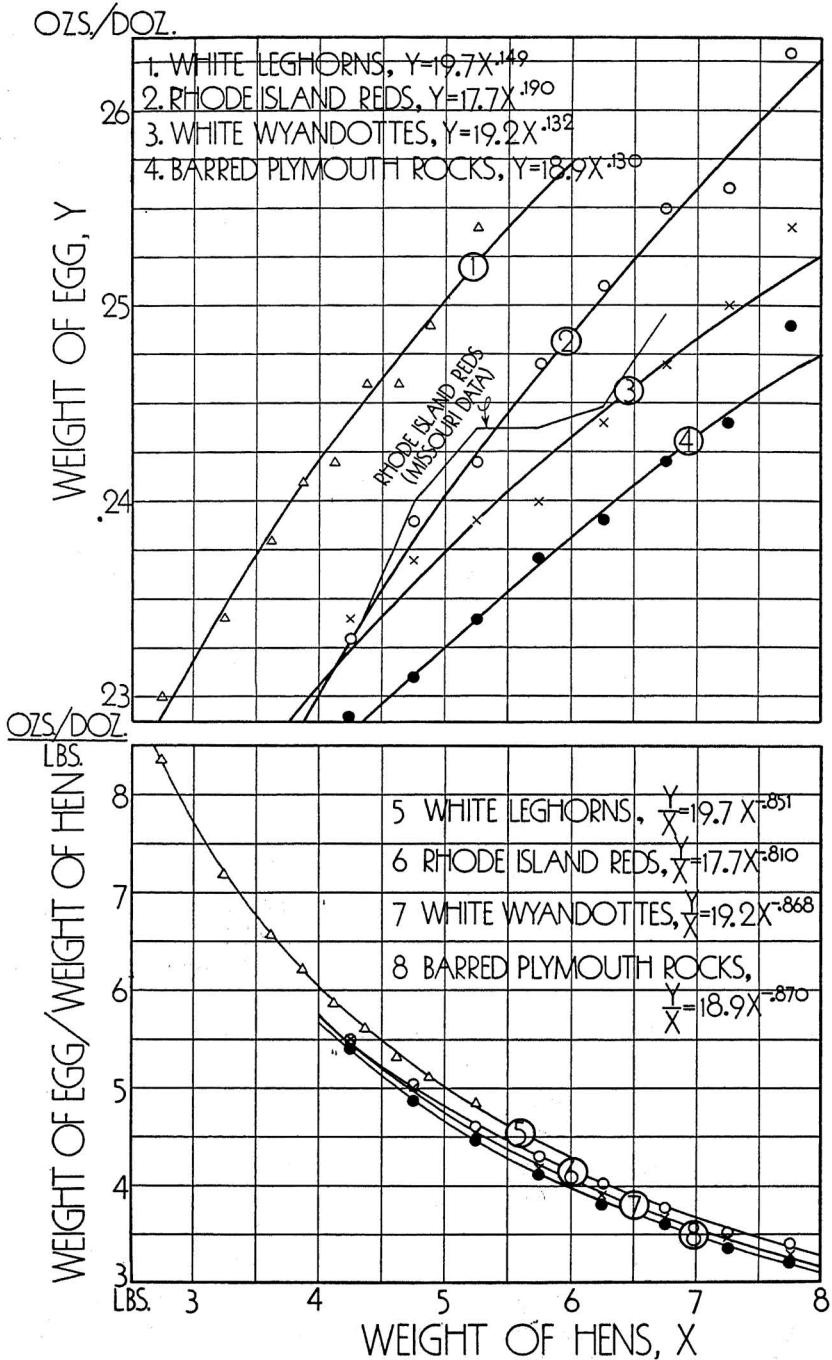


Fig. 5.—Egg weight vs. body weight in fowls. Increasing body weight 100% increases egg weight 13% to 19% (computed on the instantaneous percentage-rate basis). This increase in egg size is much below the increase of maintenance cost with increasing body size. Compare with Figs. 6, 7, and 10.

Reds, 24 ounces; for White Wyandottes,  $23\frac{3}{4}$  ounces; for B. P. Rocks, 23.25 ounces. 5-pound Leghorns thus lay eggs which are about 4% heavier than 5-pound R. I. Reds, and nearly 8% heavier than B. P. Rocks. Egg size is thus in part a characteristic of modern breeds, developed undoubtedly by selection, at least as far as Leghorns are concerned. However, within the breed, there is a definite tendency for the egg size to increase with the bird size. Thus the egg weight of an 8-pound R. I. Red is seen from Fig. 5 to be about  $26\frac{1}{4}$  ounces per dozen; of a 4-pound R. I. Red, about 23 ounces per dozen—a difference of between 10% and 19%, depending on the method employed for computing percentage differences. The equation in Fig. 5 shows the relation between egg weight (ounces/dozen) and body weight of the R. I. Red birds (pounds) to be  $Y = 17.7 X^{0.19}$ , meaning that the instantaneous percentage increase in egg weight is 0.19 times or 19 per cent of the percentage increase in body weight of the birds; in other words, when the body weight of the bird is increased by 100%, the egg weight is increased only 19% (when computed on the instantaneous change basis)<sup>17</sup>.

Evolutionary considerations would lead one to expect that size of egg would increase not with the 0.2 power as explained above, but with roughly the  $\frac{2}{3}$  to  $\frac{3}{4}$  power of body weight, as for example, surface area, basal metabolism, and maintenance cost are supposed to increase with body weight. It is reasonable to expect that the size of the egg should bear a constant ratio to the intensity of the metabolic processes of the birds, to the amount of feed it consumes for maintenance. If this is not the case, then the larger birds, producing relatively (in relation to body size) smaller eggs would be energetically less efficient egg producers than small birds; because if the egg *number* produced is the same in large and small birds, then the overhead maintenance cost per unit weight of egg would be greater in large than small birds—since the maintenance cost rises with perhaps the 0.70 power of body weight while egg size rises only with the 0.2 power.

Evolutionary considerations seem to point against the generalization that body weight as such—of course not including fat accumulation—should be a factor in the efficiency of productivity. Of course, it is possible that the unexpectedly slight increase of egg size with body size is the result of a peculiar type of selection practiced among

<sup>17</sup>The equation relating egg weight to body weight is  $Y = aX^n$ ; or  $\log Y = n \log X$ ; or  $\frac{dY}{Y} = n \frac{dX}{X}$ ; or percentage (instantaneous) change in  $Y = n$  times percentage change (instantaneous) in  $X$ . The value of  $n$  (percentage change) decreases with increasing the instantaneous intervals  $dy$  and  $dX$  to  $\Delta Y$  and  $\Delta X$ .

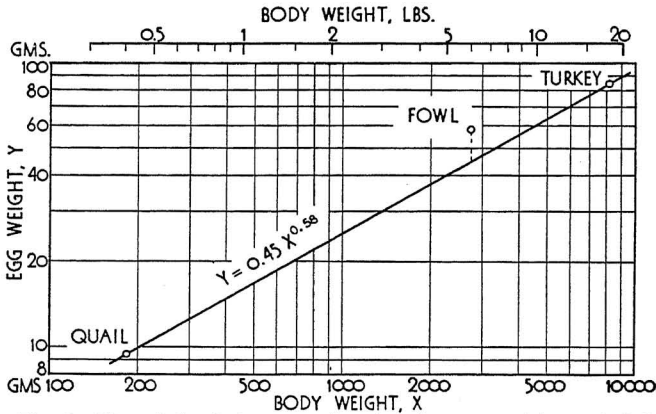


Fig. 6.—The relation between quail and turkey egg weights and their corresponding body weights. The fowl's egg seems to be relatively larger than of the turkey and quail eggs.

poultrymen. It therefore seemed interesting to compare the relation between egg size to body size in two relatively unselected species on which data could be easily secured in this Station, namely turkeys and quail. It was found that 8172 gram (18-pound) turkeys produced on the average 85 gram eggs; and 185 gram Bobwhite quail produced on the average 9.4 gram eggs. As shown in Fig. 6 the relation between egg size and body size in these two species is not 0.2, as found for fowls of different size, but about 0.6, a *very* much more reasonable value. In Fig. 6 the position of the fowl's egg—assumed to be 57 grams—is above the corresponding curve position of 44.5 grams at body weight 6 pounds.

There is a considerable literature on egg weights and body weights of different species of birds ranging from 0.6 gram humming bird eggs to 1700 gram (nearly 4 pounds!) ostrich eggs. Unfortunately the literature is very scattered. Many of these data were brought together by the remarkable physician-ornithologist, the late Dr. W. H. Bergtold, in *A study of the incubation periods of birds what determines their length?* (The Kendrick-Bellamy Co., Denver, Colorado, 1917). Fig. 7, plotted from Table 6, based largely on Bergtold's compilation, with some original data (fowls, quail, turkey, duck, goose) shows that as between different species, egg weight increase with the 0.73 power of body weight, at practically the same rate as basal metabolism. This is an exceedingly interesting result. The wide scatter of the data should not be disturbing considering the fact that in many cases the body weights were taken from one observer, and the eggs from another, and that a change in body weight due to increase or decrease in fat does not appreciably affect the *egg* size.

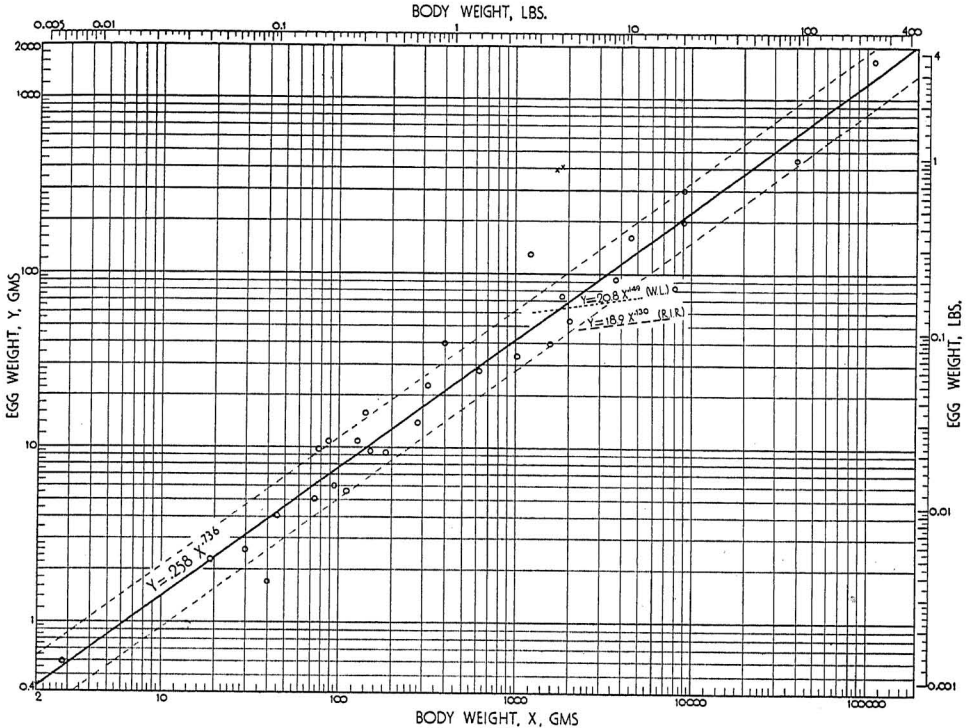


Fig. 7.—The relation between egg and body weights of different bird species ranging in body weight from 113.4 Kg. (250-pound) ostrich to a 2.8 gm. (0.10 oz.) humming bird, and ranging in egg weight from 1.7 Kg. (3½ lbs.), ostrich to 0.6 gm. (0.02 oz.) humming bird egg. Note that while within the same species, fowl, egg weight increases with the 0.13-0.2 power of body weight (Fig. 5), the relation between egg and body weight in *different* species is the same as for basal metabolism: egg weight increases with the 0.73 power of body weight. The X<sup>s</sup> (Kiwi) are not included in equation. With the exception of the data for the quail, turkey, goose, and duck, the data were plotted from Bergtold's compilation (see text). The numerical data (first value gm. body weight, second, gm. egg weight) are: Ostrich (113, 380-1700); Emperor Penguin (40,817-454); Toulouse goose (9072-200.8); California vulture (9070-309); Turkey (8172-85); Chinese goose (4536-165.4); Pekin duck (3629-94.5); one domestic fowl included in general equation (2041-72); Runner duck (1814-75.6); Kiwi—*not included in equation* (1814-411 and 1701-397); guinea hen (1587-40); Adelle penguin (1205-130); Ring-neck pheasant (1020-34); Golden pheasant (624-28); yellow-billed tropic bird (397-40); long-eared owl (320-23); domestic pigeon (283-14); quail (185-9.4); Magpie (151-9.6); Screech owl (142-16); mourning dove (128-11); Meadow lark (113-5.7); Western robin (95-6.0); Killdeer (88-11); Western nighthawk (78-9.9); Brewer's blackbird (74-5.1); Kingbird (45-4.1); Catbird (40-1.7); English sparrow (30-2.6); House finch (19-2.3); Broad-tailed humming bird (2.8-0.6). The broken flattish curves with accompanying equations are reproductions in terms of egg weight (grams) vs. body weight (grams) of the curves for White Leghorn (W. L.) and R. I. Red (R. I. R.) fowls in Fig. 5 which emphasize the great difference in slope (exponent) for inter and intra species. The two broken curves on each side of the average heavy line represent the standard error of estimate, including % of the data.

However, the 0.73 power relation does not hold for the egg-body size relation in domestic fowls. Within the species, egg weight increases not with the 0.7 but 0.15 power of body weight. It appears that the larger size of eggs from larger fowls can not compensate the greater maintenance cost of larger birds. As previously noted in order to make such compensation, the egg weight would have to increase with increasing body weight at the same rate as maintenance cost. We

assumed in our partition equation (7) that maintenance cost increases with the 0.73 power of body weight, while egg size increases only with about the 0.2 power of body weight—a difference which leads one to conclude that larger fowls must produce more eggs than small if efficiency of production is the same in large and small. We must therefore next consider the influence of body size on productive level of fowls\*

**b. Egg number and production vs. body weight:** Fig. 8 shows how the average egg *number* production changes with increasing body weight of fowls. The egg production number appears to increase until a definite body weight characteristic of the group and breed is reached, then to decline. Thus in curve 3 (Fig. 8) representing the Mass. R. I. Red data, the egg production remains roughly constant at the 190-egg level between 4 and 5½ pounds live weight, then it drops steeply down to the 100-egg level when body weight 8½ pounds is reached—a tremendous reduction. Each breed and group of birds is seen in Fig. 8 to have its characteristic optimum body weight where egg production is a maximum. Decline from this maximum is of course the resultant of the development of some unfavorable situation, perhaps accumulation of unnecessary fat which interferes with the optimum functioning of the body in general and the reproductive system in particular.

\*Addendum: The following data on the relation between bird weight, egg weight, and hatching weight of the birds on his farm, were sent by Mr. E. B. Powell, Manager Experimental Farm, Purina Mills, St. Louis, Missouri, after Fig. 7 was prepared. The pigeons were incubated by their parents, the turkeys and ducks in a commercial incubator. The data include 21 Bronze turkeys and 38 of their poults; 53 White Holland Turkeys, their eggs and poults; 100 ducks; 16 pigeons with their 43 eggs and squabs.

Bird	Bird Weight gms.	Egg Weight gms.	Hatching Weight gms.	Ratio
				Hatching Weight Egg Weight
Bronze Turkey	7280 (16.1 lbs.)	88.5	59.0	67%
White Holland Turkey pullets	5865 (12.9 lbs.)	80.3	53.1	66%
White Pekin Ducks	3452 (7.6 lbs.)	94.4	59.0	63%
Red Carneau Pigeons	481 (1.1 lbs.)	23.7	20.0	84%

These data for the pigeon fall almost exactly on the general line in Fig. 7. The turkey eggs on the other hand are considerably below the line, as were the turkey-egg data in Fig. 7 (According to Fig. 7, the pigeon egg weighs 24 grams; Pekin duck egg, 104 grams, turkey egg, 180 for the Bronze and 153 for the Holland. The turkey egg is, in relation to the turkey weight, very small by comparison with, for example, the White Leghorn fowl egg.)

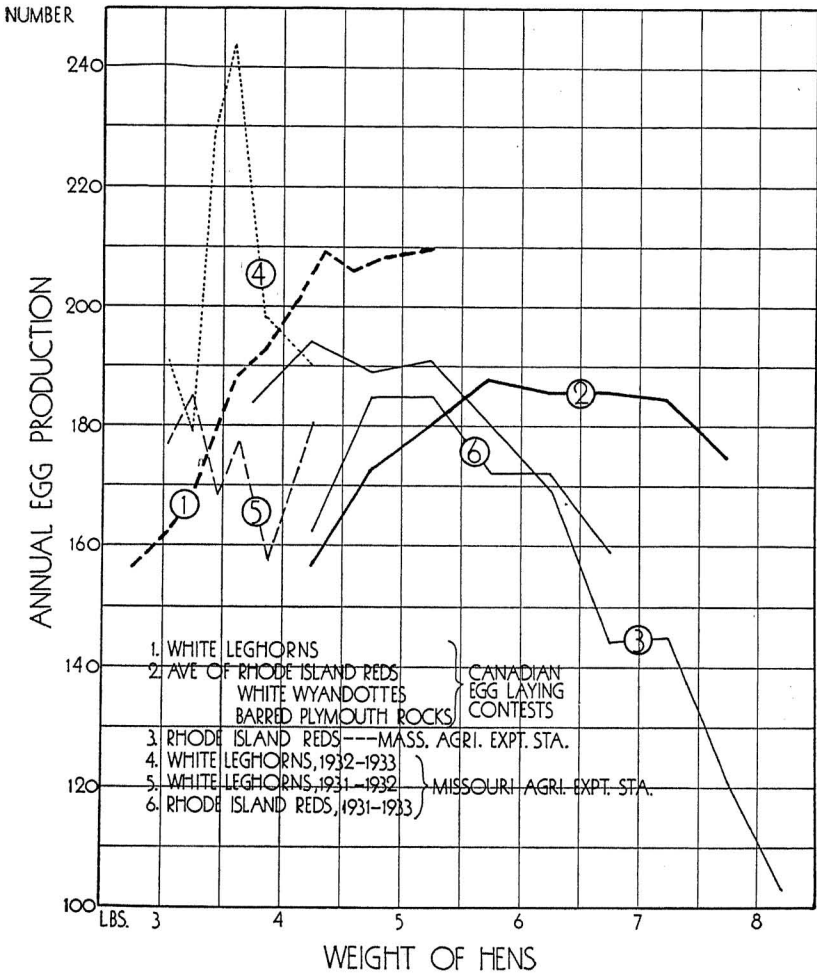


Fig. 8.—Rise and decline in egg production with increasing body weight. Each group of birds produces maximum at a characteristic body weight.

Let us consider the increasing production *preceding the peak level*. What is the course of the *increasing* production with increasing body weight? Or to phrase it more boldly, what is the “law” relating egg production with increasing body weight on its path to peak production?

Our own data, plotted in Fig. 2, not satisfactory because of extremely low production for reasons previously explained, indicate that production (in terms of grams of egg produced per day) increases with the 0.89 power of body weight for the Leghorns, and

with the 0.31 power for the R. I. Reds. The great difference between the constants for these two breeds of fowls housed under the conditions previously described makes it impossible to draw conclusions concerning the "law" relating egg production to body weight.

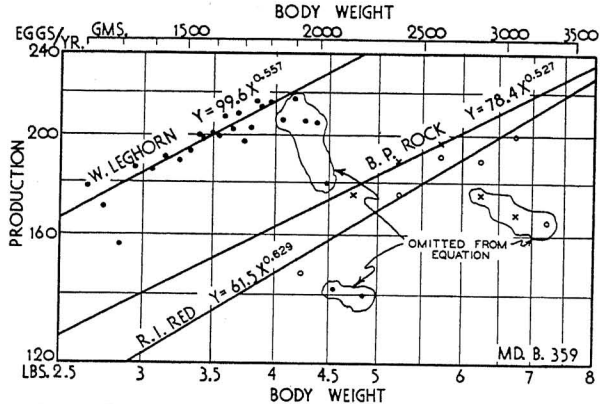


Fig. 9.—Rise in egg production *number* with increasing body weight in the Maryland-contest fowls, plotted on a logarithmic grid. The equations were fitted to the data for the rising phase only.

We next present an analysis of the relation between egg production—*number* of eggs per year—and body weight in the Maryland Egg Laying Contest (Maryland Agr. Exp. Sta. Bul. 359). The results on the three breeds presented in Fig. 9 are satisfactorily consistent. Fig. 9 leads to the conclusion that prior to peak production, egg production (*number* per year) increases with, roughly, the 0.6 power of body weight. In other words, the egg production increases about 0.6 times as rapidly as body weight; that is an increase in body weight by 100% tends to be associated with increasing egg production by about 60% (on the instantaneous-rate basis,  $\frac{dY}{Y} = \frac{0.6 dX}{X}$ ).

This generalization holds true for the light Leghorns as also for the heavier breeds in spite of the considerable differences in the absolute production level of the light and heavy breeds.

It is recalled that this generalization holds true only for the phase of production preceding a characteristic body weight, which appears to be about 4 pounds in the Leghorns and 5½ pounds in the B. P. Rocks and R. I. Reds.

The results of our analysis of the relation between egg production and body weight of the Canadian Contests (Bul. 139 of the Department of Agriculture, Dominion of Canada, Ottawa) are presented in Fig. 10. The upper curves show that the egg-production *number*



increases (preceding the peak level) with the 0.67 power of body weight in Leghorns, and 0.55 power in the heavier breeds. The result on the Canadian contest confirms the results on the Maryland contest to the effect that prior to peak production the egg production number tends to increase with the 0.6 power of body weight.

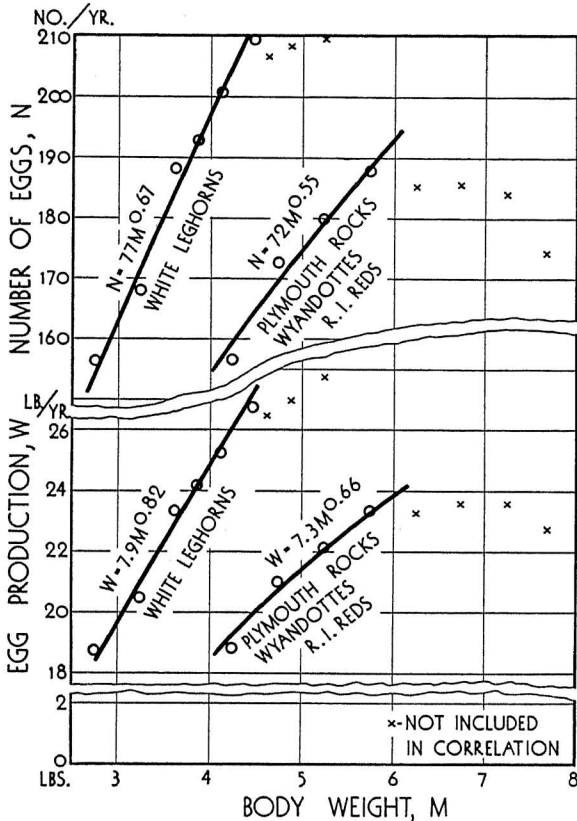


Fig. 10.—Rise in egg-production number and also in weight with increasing body weight in the Canadian-Contest fowls plotted on an arithmetic grid. The equations were fitted to the data for the rising phase only.

Since the weights of individual eggs tend to increase with increasing body weight, then egg production in terms of *weight* per year would increase more rapidly with increasing body weight than production in terms of *numbers*. The lower curves in Fig. 10 demonstrate that the egg production in terms of *weight* increases with the 0.82 power of body weight in Leghorns (as compared to the 0.67 power in terms of egg numbers), and 0.66 power in the heavy breeds (as compared to the 0.55 power in terms of egg numbers). The

peak production appears to be reached at about  $4\frac{1}{4}$  pounds body weight for the Leghorns and  $5\frac{3}{4}$  for the heavier breeds. (For the Maryland data the peak was estimated to be about 4 pounds for the Leghorns, and  $5\frac{3}{4}$  pounds for the heavier breeds.)

#### 4. Influence of Feed Consumption Level on Efficiency of Egg Production, and of Egg Production Level on Feed Consumption

The inherited egg-production urge with the consequent drainage of nutrients from the blood stream, presumably conditions the fowl's hunger and appetite for food. *A priori* considerations lead to the conclusion that if the fowl does not change in body weight, the feed consumption level (above maintenance) must increase at least in direct proportion with increasing production. (According to the diminishing increments theory of Jull, Titus, Hendricks et al., increase in feed consumption would be expected to be more rapid than increase in egg production.) And since, as shown in Fig. 1, gross efficiency tends to be proportional to egg production (this is not strictly true, see Fig. 1), gross efficiency should also tend to be proportional to feed consumption. It is instructive to plot feed consumption against egg production (Fig. 11) to get a visual impression of the interrelation between the two, and also gross efficiency against feed consumption (Fig. 4). Fig. 11 shows that, for the Leghorns at any rate, feed consumption is nearly a linear function of egg production. The Leghorn equation indicates that the maintenance cost (not counting egg production cost) of the average bird is 55.7 pounds, or 25.3 Kg., or 76,000 Calories per year (or 0.15 lbs. or  $2\frac{1}{2}$  ounces or 69 grams or 208 Calories per day). The additional cost of producing an average egg (not counting maintenance) is 0.122 pounds or 55.4 grams, or 166 Calories, about 2 ounces—nearly as much as it costs to maintain a hen. These last figures give us another basis for computing the *net* energetic efficiency of egg production, that is, the efficiency (with respect to TDN) of the ovary-oviduct system not including maintenance cost. If a 56-gram egg has a fuel value of  $56 \times 1.6 = 90$  Cal., and if 166 Cal. TDN is expended for producing the egg (not counting maintenance), then obviously the net efficiency of egg production is  $\frac{90}{166} \times 100 = 54\%$ . This value is identical to the average value we found for the net efficiency of milk production of 368 dairy cows (see lower average, page 21, Missouri Agr. Exp. Sta. Res. Bul. 238, showing that the *net* efficiencies of individual

groups vary from 43 to 82%, but that the average is 54%). We believe that the closeness of the net-efficiency values for egg and milk production is more than a coincidence.

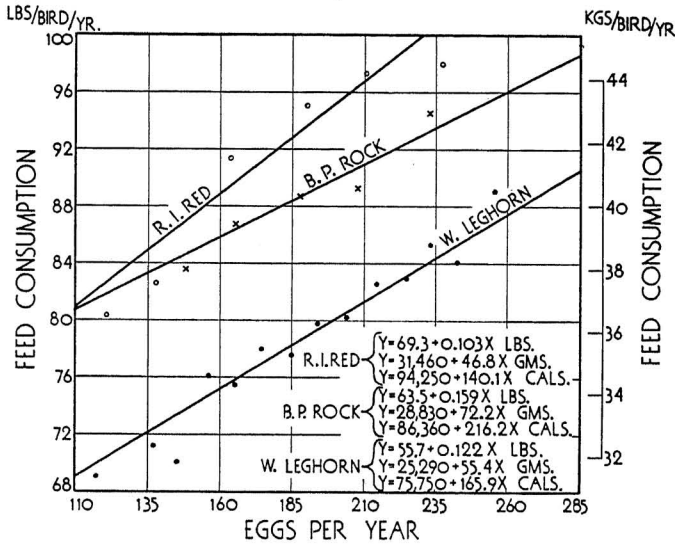


Fig. 11.—Feed consumption as function of egg production number.

The R. I. Red and B. P. Rocks data are fewer in number, and the nature of their distribution is therefore less definite. Linear equations were forced on them with the resulting equations shown in Fig. 11. The numerical values of the constants are reasonable enough.

Fig. 4 shows, as might have been foreseen, that relating gross efficiency to feed consumption practically duplicates the relation of feed consumption to egg production, except of course that the order of the curves is reversed. The Leghorns which consumed least feed of the three breeds for a given egg-production number, have the highest efficiency. If body weight remains constant, the gross efficiency increases with feed consumption because egg production increases with feed consumption (or feed consumption increases with egg production) and efficiency increases with egg production.

Incidentally, the efficiency and feed-consumption curves in Fig. 4 demonstrate strikingly what is of course known, that the feed is less, or overall efficiency is greater, for producing a given number of eggs in small than large fowls *producing the same number of eggs of the same size per year*. The reason for this fact is of course that more feed is expended for maintaining the large than the small fowl.

If the large fowl is to be as efficient as the small producing the same number of eggs, the egg size from the large fowl must exceed that from the small fowl by the amount of extra maintenance cost of the large over the small fowl. Thus if the maintenance cost of birds increases with the 0.73 power of body weight, then the egg size should likewise increase with the 0.73 power of body weight. Since we previously demonstrated that egg size in domestic fowls increases not with the 0.73 but with the 0.2 power of body weight (at least in different-sized birds of the same breed), it must be concluded that for equal efficiency not only the size but also the number of eggs must be greater in large than small fowls.

### 5. Comparison Between Efficiencies of Egg Production and Growth

We defined overall or gross energetic efficiency by the ratio

$$\frac{\text{Egg energy produced}}{\text{TDN energy consumed}}$$

and we found that "good" layers (260-egg birds) produce eggs at an efficiency of about 20%. It is instructive to compare the gross efficiency of egg production with that of growth. We already pointed out that the gross efficiency of milk production of "good" dairy cows is of the order of 30%, and that the *theoretical maximum* efficiency of muscular work in horses (pulling loads on a horizontal platform) is about 24%, but that the average 24-hour efficiency of horses when working 8 hours a day is of the order of 13 per cent. We shall complete this comparison by a brief discussion of the energetic efficiency of growth.

According to Terroine and Wurmser's computations the average gross efficiency of embryonic growth of the chick and silk worm is 60% to 70%, that is, about thrice as great as of egg production of "good" layers. However, embryonic growth and egg production are expressed in different units; in embryonic growth efficiency is computed with reference to egg yolk, while in egg production it is computed with reference to TDN. Gross efficiency of postnatal growth is much less. According to Rubner, gross efficiency of early postnatal growth is about 34%. (According to Rubner, 4.8 Calories are required to produce 1 gm. of body substance containing 1.7 Calories.

The gross efficiency is therefore  $\frac{1.7}{4.8} = 34\%$ .) The following brief examination of growth data indicates that on "ordinary" diets growth efficiency tends to fall below 34%, particularly in the later ages. Efficiencies of the order of 34% are obtained only on excellent diets.

For convenience of computation we assumed that 1 gram of body weight uniformly contains 2.0 (rather than 1.7) Calories, and 1 gram of TDN contains 4 Calories. Employing these factors, the percentage gross efficiency of growth of chickens, computed from data by Card and Kirkpatrick (Storrs Bul. 96) declines from 21-25% 1st week, to 3-5% 24th week.

PERCENTAGE GROSS EFFICIENCY OF GROWTH OF CHICKENS (1 gm. feed = 3 Cal.; 1 gm. weight gain = 2 Cal.).

Age, Weeks	1	2	3	4	5	6	7	8	9	10	11	12
W. Leghorns	26	22	19	21	18	20	19	16	10	13	9	15
R. I. Reds	21	17	25	17	22	19	19	18	20	17	12	15

Age, Weeks	13	14	15	16	17	18	19	20	21	22	23	24
W. Leghorns	8	8	8	9	6	7	4	8	7	3	5	2
R. I. Reds	5	10	10	7	10	5	7	9	7	7	5	5

We are indebted to Professor Gustave F. Heuser for sending us unpublished data from the Poultry Department, Cornell University, on unusually rapid growing chicks and the amount of feed consumed by them, from which we computed the following growth efficiency values. In these computations we assumed that the energy content of 1 gm. of their feed was 3 Cal. TDN, and 1 gm. weight-gain 2 Calories. The 1st group was composed of 10 males and 14 females; the 2d group, 15 males and 10 females.

PERCENTAGE GROSS EFFICIENCY OF GROWTH OF CHICKENS (1 gm. feed = 3 Cal.; 1 gm. weight-gain = 2 Cal.).

Age, weeks	1	2	3	4	5	6	7	8
Efficiency, Group 1	34.8	38.3	33.3	31.8	28.8	23.4	18.2	25.7
Efficiency, Group 2	28.9	38.6	32.6	32.8	29.1	28.2	21.8	23.7

If our conversion factors are roughly correct, then the gross energetic efficiency of growth of these rapidly growing chicks on the given diet (Diet: yellow cornmeal 57.75 group 1 and 57.25 group 2; wheat flour middlings 20.00; egg white 10.25 group 1 and 8.25 group 2; dried liver 7.50 group 1 and 10.0 group 2; cod liver oil 1; steamed bone meal 2.00; limestone 1.00; salt 0.50.) is rather higher than of egg production, and is of the same order as the gross energetic efficiency of milk secretion.

It is interesting to note that the growth efficiency of early post-natal growth of rats and of cattle is not very different from that of chickens.

Percentage gross efficiency of growth of young rats on an optimum diet may be computed from data by Palmer et al. (Minn. Tech. Bul. 92).

PERCENTAGE GROSS EFFICIENCY OF GROWTH OF YOUNG RATS (1 gm. dry matter in food = 5.2 Calories; 1 gm. weight gain = 2 Calories.).

Weeks	146 Males						141 Females					
	1	2	3	4	5	6	1	2	3	4	5	6
Efficiency	25	23	21	20	19	18	23	19	17	15	14	13

Percentage gross efficiency of growth of dairy cattle, based on data in the University of Missouri herd is given below:

PERCENTAGE GROSS EFFICIENCY OF GROWTH (1 gm. TDN = 4 Cal., 1 gm. weight gain = 2 Calories.).

Age Months	1	2	3	4	5	6	7	8	9	10	11	12
Holstein heifers	35	26	33	23	18	17	13	13	10	10	11	9
Jersey heifers	37	25	30	26	20	20	13	13	11	9	9	9

Age Months	13	14	15	16	17	18	19	20	21	22	23	24
Holstein heifers	8	9	8	7	7	7	6	6	6	4	8	7
Jersey heifers	8	8	6	6	7	7	5	7	5	5	7	6

The characteristic feature about the gross efficiency of growth is that it declines rapidly with increasing age. Some of the decline in growth efficiency with increasing age is only apparent due to the decrease in water concentration in the body. But most of it is real because the older the animal and the greater its size, the greater the maintenance expense of the body in comparison to weight gain. In other words the phrase "growth efficiency" is indeterminate without the modifying statement of age, or body weight and growth rate. The energetic efficiency of a living converter is thus dependent on two factors: (1) maintenance cost which in turn depends on the size of the animal; (2) speed of the converting process which is often in turn dependent on the structural complexity of the process. Differences in efficiency of biologic transformation in productive processes—as egg or milk production, or growth, can usually be traced to these determining factors. Thus egg production is less efficient than early growth, because whereas egg production includes the overhead maintenance cost of the fowl that produced the egg, growth of the chick does not include the overhead maintenance cost of its mother. With increasing age however a maintenance charge is built up by the increasing size of the body with a consequently decreased gross efficiency.

## VI. SUMMARY AND CONCLUSIONS

One of the major questions this research has set out to answer is: "What is the relative *net* and *gross* efficiency of egg production as compared to the corresponding efficiencies for milk production, growth, and muscular exercise (on which reports from this station have been previously published) and what is the influence of live weight thereon?" The conclusions are:

(1) Prior to a certain body weight at which production is at maximum (about 4 pounds in Leghorns,  $5\frac{3}{4}$  pounds in R. I. Reds and B. P. Rocks) the energetic efficiency of egg production is practically independent of live weight. This conclusion on egg production is similar to the preceding on milk production and muscular work. Following this characteristic weight of maximum production, efficiency and profit decline.

(2) The distribution of the consumed feed between the three principal uses—egg production, maintenance, body weight changes—is given for our data on an extremely low-producing group of birds by the equation  $\text{Feed} = 0.692 (\text{egg}) + 0.300 M^{0.73} + 1.1 \Delta M$  indicating that on the average 0.692 grams of feed was expended for producing 1 gram egg (including shell); 0.30 grams feed was expended per  $M^{0.73}$  grams body for maintenance, assuming that maintenance cost varies with the 0.73 power of body weight,  $M$ ; 1.1 grams feed was expended for increasing body weight by 1 gram. The *overall or gross* efficiency (including maintenance cost) of egg production was computed from the ratio  $\frac{\text{gm. whole egg produced} \times 1.6}{\text{feed consumed} \times 3}$ , assuming that 1 gram whole egg (including shell) is equivalent to 1.6 Cal., and 1 gram feed contains 3 Cal. TDN. The *net* energetic efficiency (not counting maintenance cost) may be computed from the above equation, namely  $\frac{1.6}{0.692 \times 3}$  or nearly 80%. But using other data (see Table A in appendix and discussion on pp. 46-7) the net efficiency was computed to be about 60%, which is of the same order as that we previously reported for milk production in dairy cattle.

(3) The overall or *gross* energetic efficiency of egg production of course increases with the egg production level because of decrease of overhead maintenance cost per unit egg. Thus in Leghorns, the gross efficiency (with respect to TDN consumption), is of the order of

11% for 100-egg producers, 14% for 150-egg producers, 17% for 200-egg producers, 20% for 250-egg producers, and 27% for 360-egg producers. These values are about  $\frac{1}{2}$  the efficiency levels attained by dairy cows of roughly corresponding productive levels.

(4) The *net* energetic efficiency of egg production appears to be on the contrary, the same as the net efficiency of milk production. In other words, the energetic efficiency of the oviduct—ovary system for egg production appears to be of the same order as of the mammary gland for milk production, but the overhead maintenance cost for a given productive level is relatively greater for fowls than for cows with consequently lower *gross* energetic efficiency for egg production.

How should one explain this anomaly that the *net* efficiency (not counting maintenance) is the same for egg as for milk production while the *gross* or overall (including maintenance expense) efficiency of egg production is only about half that of milk production? It is suggested that there is a greater time element in egg than milk production, because of the greater organizational complexity of egg than of milk; and since time is inseparable from maintenance cost, there is also a greater overhead maintenance expense and consequently lower energetic efficiency in egg than milk production. Other possible contributing factors to the efficiency differences in egg and milk production are discussed in the text.

(5) The gross energetic efficiency of egg production (with respect to TDN consumption) is of the same order as the gross energetic efficiency of growth on "ordinary" diets (20%-25% during 1st week after hatching; 8-10% during 15th week after hatching) and is considerably below growth efficiency on excellent diets (35% during 1st week after hatching to 25% during 8th week). The smaller gross efficiency of egg production than early growth is understandable in view of the large overhead cost of maintaining the hen that lays the egg—an overhead which the young chick does not have. Of course the more grown the bird, the greater becomes the overhead expense for the grown part, and consequently growth efficiency rapidly declines with increasing size.

(6) Incidentally it was found that the fuel value (in a bomb calorimeter) of egg and shell is 1.6 Cal. per gram (in 58-gram eggs); and that while egg size within a species (fowl) increases with the 0.15 power of body weight, egg size between different species increases with the 0.73 power of body weight.



## APPENDIX

**Table A**

**Table B**

**Figs. 12, 13a, 13b, and 14.**

TABLE A.—SUMMARY OF OUR DATA BY 28-DAY PERIODS AND BY

Date of 28-day period	No. of birds	Av. Live Weight gms.	Av. Daily Live Wt. Gain (±) gms.	Eggs per bird	Average daily egg production			Av. daily feed consumption		Per Cent TDN Calories Consumed	
					gms./day	Cal./day	Per cent of possible production	gms./day	TDN Cal./day	Maintenance	Observed Eggs
<b>1934</b>											
4-14 to 5-11	51	2557	-11.5	13.71	27.1	43.4	49.0	98.5	295.5	86.1	14.7*
5-12 to 6- 8	47	2069	-10.0	6.85	11.5	18.4	24.5	70.2	210.6	107.5	8.7
6- 9 to 7- 6	47	1948	4.5	9.60	17.7	28.3	34.3	72.4	217.2	77.5	13.0
7- 7 to 8- 3	44	1998	0.4	5.32	9.5	15.2	19.0	61.2	183.6	85.8	8.3
8- 4 to 8-31	45	2018	2.7	6.49	12.2	19.5	23.2	74.4	223.2	85.3	8.7
9- 1 to 9-28	44	2124	5.4	4.16	7.9	12.6	14.9	85.3	255.9	82.4	4.9
9-29 to 10-26	41	2221	0.3	3.90	7.7	12.3	13.9	82.1	246.3	87.4	5.0
10-27 to 11-23	38	2226	2.1	1.16	2.3	3.7	4.1	85.4	256.2	91.8	1.4
11-24 to 12-21	53	2148	5.1	.74	1.3	2.1	2.8	87.6	262.8	88.4	0.8*
Total	410			53.21							
Yearly Average (a)	45.6	2148	- 0.3	5.91	11.1	17.8	21.1	79.9	239.7	88.0	7.4
<b>1935</b>											
12-22 to 1-18	51	2224	2.1	3.10	5.7	9.0	11.1	96.9	290.7	91.3	3.1
1-19 to 2-15	51	2218	1.0	4.57	6.6	10.6	16.3	91.4	274.2	87.0	3.1
2-16 to 3-15	47	2295	- 0.4	5.19	10.2	16.3	18.5	93.0	279.0	86.1	5.1
3-16 to 4-12	45	2283	- 1.9	4.00	7.5	12.0	14.3	82.5	274.5	99.2	4.1
4-13 to 5-10	Data incomplete										
5-11 to 6- 7	44	2184	- 1.5	10.75	20.1	32.2	38.4	95.0	285.0	90.4	11.3
6- 8 to 7- 5*	38	2397	- 2.5	9.71	16.3	26.1	31.4	92.6	277.8	94.7	9.4
7- 6 to 8- 2*	38	2119	- 0.8	7.92	14.0	22.4	28.3	75.1	225.3	89.7	9.9
8- 3 to 8-30*	38	2100	0.1	5.42	6.7	10.8	19.4	51.7	155.1	99.0	7.0
8-31 to 9-27	36	2011	- 1.0	3.86	6.7	10.7	13.1	69.0	207.0	93.6	5.2
10-11 to 11- 7	59	2134	0.8	3.36	6.1	9.7	12.0	80.8	242.4	86.4	4.0
11- 8 to 12- 5	60	2149	0.8	7.98	15.4	24.6	28.5	102.1	306.3	91.2	8.0
12- 6 to 1- 2	58	2238	4.3	10.38	21.2	33.9	10.4	118.6	355.8	90.3	9.6*
Total	451			54.00							
Yearly Average (a)	50.1	2204	0.7	6.00	12.0	19.2	21.4	93.4	280.2	90.4	6.9
Total (b)	565			76.08							
Yearly Average (b)	47.1	2198	- 0.3	6.34	11.5	18.4	22.6	89.3	267.9	91.2	6.9
<b>1936</b>											
1- 3 to 1-30	104	1973	- 0.2	8.09	15.7	25.1	28.6	82.1	246.3	87.0	10.2
1-31 to 2-27	95	2019	0.3	6.41	12.7	20.3	22.9	86.5	259.5	90.0	7.8
2-28 to 3-26	90	2040	- 0.5	8.47	16.9	27.0	30.3	94.1	282.3	85.3	9.5*
3-27 to 4-23	80	2068	- 1.0	9.41	18.8	30.1	33.6	97.2	291.6	88.6	10.3
4-24 to 5-21	80	2062	- 0.1	9.50	18.9	30.3	33.9	85.4	256.2	81.5	11.8
5-22 to 6-18	70	1998	- 2.6	8.43	16.8	26.9	30.1	73.9	221.7	86.8	12.1
6-19 to 7-16	65	1954	- 2.9	5.46	10.4	16.6	19.5	60.7	182.1	91.1	9.1
7-17 to 8-13	59	1943	- 0.8	1.75	3.2	5.1	6.3	59.0	177.0	95.9	2.9
8-14 to 9-10*	51	1912	- 2.1	1.29	2.4	3.8	4.6	65.6	196.8	97.3	1.9
9-11 to 10- 8	52	1889	- 4.5	.27	0.5	0.8	1.0	65.2	195.6	100.5	0.4
10- 9 to 11- 5	92	1911	4.7	2.87	5.7	9.0	10.3	89.9	269.7	89.8	3.4*
11- 6 to 12- 3	83	2060	2.6	4.64	9.7	15.5	16.6	98.0	294.0	93.5	5.3
12- 4 to 12-31	80	2147	2.4	3.50	7.1	11.4	12.5	107.4	322.2	95.0	3.5
Total (a)	950			72.20							
Yearly Average (a)	79.2	2010	0.1	6.02	11.9	19.0	21.5	85.1	255.3	89.9	7.4
Total (b)	1001			75.09							
Yearly Average (b)	77.0	2005	0.0	5.78	11.5	18.4	20.4	84.1	252.3	90.3	7.3
<b>1937</b>											
1- 1 to 1-28	75	2246	0.8	4.41	9.2	14.7	15.8	93.5	280.5	93.5	5.2*
1-29 to 2-25	70	2321	1.1	4.93	10.1	26.2	17.6	96.4	289.2	91.6	9.1
2-26 to 3-25	66	2294	- 3.4	4.80	10.1	16.2	17.1	99.2	297.6	96.1	5.4
3-26 to 4-22	65	2280	- 0.3	3.54	7.2	11.6	12.6	100.6	301.8	95.1	3.8
4-23 to 5-20	63	2287	- 1.1	3.75	7.4	11.8	13.4	94.3	282.9	96.3	4.2
5-21 to 6-17	47	2399	0.8	7.06	14.2	22.7	25.2	93.3	294.9	96.6	7.7
6-18 to 7-14*	46	2364	- 2.5	8.48	16.9	27.1	30.3	93.2	294.6	86.5	9.2
7-15 to 8-11*	42	2278	- 2.7	6.62	15.0	23.9	23.6	99.6	298.8	93.4	8.0
8-12 to 9- 8*	40	2248	- 0.4	6.85	13.2	21.1	24.1	80.3	240.9	92.0	8.8*
9- 9 to 9-30**	38	2227	- 2.0	3.24	6.6	10.6	11.5	104.2	312.6	94.7	3.4*
Total (a)	424			26.81							
Yearly Average (a)	60.6	2292	- 0.4	3.83	9.1	14.6	16.2	97.6	292.8	95.0	5.0
Total (b)	552			54.11							
Yearly Average (b)	55.2	2294	- 0.8	5.41	10.6	17.0	18.5	96.5	289.5	94.3	6.3
Total (c)	2235										
Average (c)	60.4	2128	0.5		11.2	17.9	20.6	88.2	264.6	—	6.8

\*Months omitted in calculating equations.

\*\*21-day period.

(a) Excluding months omitted in calculating equations.

(b) Including months omitted in calculating equations.

(c) All periods excluding months omitted in calculating equations.

Column 7 = column 6 × 1.6

Column 8 =  $\frac{C. 5}{C. 2 \times 28}$

Column 10 = C. 9 × 3

Column 11 =  $\frac{C. 21 (\Sigma \text{Weight})}{\Sigma \text{feed}}$

Column 12 =  $\frac{C. 7}{C. 10} \times 100$

YEARS, INCLUDING PARTITION-EQUATION CONSTANTS

Energetic Efficiency, %			Profit per 28 days, dollars				Constants of Equation Feed = B (Eggs) + C (Weight) <sup>0.73</sup> + D (Gain ±), gms.				
Av. Observed	Av. served	Gross	Per Bird	Per Kg. Live Wt.	Per Doz. Egg	Per 100 lbs. Feed	B	C	D	Sr	R
Not Corrected	Corrected	Computed									
Weight Gain 13	Weight Gain 14	Net 15	16	17	18	19	20	21	22	23	24
14.67	12.64	49	0.164	0.064	0.144	2.69	1.0331	0.2766	1.3661	23.26	0.6664
8.12	7.13	57	0.056	0.027	0.098	1.29	0.9270	0.2925	1.5133	17.05	0.7793
13.02	13.78	76	0.111	0.057	0.139	2.47	0.7005	0.2241	0.3756	13.70	0.4423
8.26	8.15	53	0.036	0.018	0.081	.93	1.0147	0.2054	1.8531	10.46	0.7531
8.71	8.86	66	0.044	0.022	0.081	.94	0.8140	0.2469	0.4617	12.84	0.7655
4.93	5.65	(99)	-0.018	-0.009	-0.052	-.36	0.5357	0.2635	1.9791	11.71	0.8699
4.99	5.01	41	-0.019	-0.009	-0.058	-.40	1.3061	0.2602	1.3433	10.86	0.8486
1.45	1.53	52	-0.081	-0.040	-0.342	-1.54	1.0312	0.2845	2.0649	14.26	0.8593
0.82	0.91	59	-0.092	-0.043	-1.513	-1.72	0.9110	0.2902	1.6934	14.33	0.8206
7.4	7.18	61	0.025	0.011	0.051	0.497					
3.14	3.23	64	-0.006	-0.003	-0.213	-.92	0.8334	0.3210	1.3233	13.64	0.7933
5.20	5.31	49	-0.002	-0.001	-0.046	-.32	1.0933	0.2885	1.8026	13.37	0.8413
5.87	5.85	43	-0.001	0.000	-0.015	-.12	1.2487	0.2844	0.8323	13.78	0.7069
4.85	4.58	78	-0.002	-0.001	-0.055	-.37	0.7287	0.2917	2.4846	16.15	0.7082
11.39	11.15	(103)	0.047	0.022	0.119	1.82	0.5168	0.3159	1.3063	15.51	0.6969
9.55	9.25	(137)	0.069	0.029	0.094	1.20	0.3886	0.3240	1.1792	16.11	R <sup>2</sup> neg.
10.09	9.91	(98)	0.073	0.034	0.110	1.66	0.5502	0.2529	1.7916	12.63	0.2431
7.00	7.01	—	0.049	0.024	0.109	1.54	-0.0086	0.2890	2.0107	6.74	0.9853
5.18	5.09	65	-0.009	-0.004	-0.029	-.22	0.8224	0.2519	1.1170	17.70	0.7609
4.04	4.09	36	-0.030	-0.014	-0.107	-.60	1.5036	0.2606	1.2447	11.75	0.7338
8.06	8.13	(108)	0.041	0.019	0.061	.64	0.4959	0.3453	1.1584	12.80	0.8356
9.55	9.78	(134)	0.070	0.031	0.081	.95	0.3975	0.3865	0.5620	18.51	0.7730
6.9	6.40	76	0.013	0.006	0.020	0.168					
6.9	6.87	—	0.024	0.011	0.042	0.385					
10.37	10.37	88	0.070	0.036	0.100	1.32	0.6086	0.2805	0.8120	15.11	0.6400
7.82	7.86	85	0.027	0.013	0.050	.50	0.6293	0.3030	1.4801	12.93	0.8293
9.55	9.47	61	0.061	0.030	0.085	1.03	0.8683	0.3085	1.6318	10.43	0.9145
10.43	10.34	92	0.077	0.037	0.097	1.27	0.5824	0.3289	0.8333	11.45	0.6141
11.87	11.85	65	0.093	0.045	0.117	1.76	0.8354	0.2661	1.0892	8.94	0.8394
12.16	11.62	69	0.085	0.042	0.120	1.85	0.7760	0.2516	1.2907	10.29	0.8933
9.09	8.65	64	0.039	0.020	0.086	1.04	0.8362	0.2205	1.1029	10.60	0.8583
2.85	2.79	43	0.000	0.000	-0.251	-1.00	1.2317	0.2265	1.3706	9.71	0.8557
2.00	2.02	—	-0.005	-0.003	-0.500	-1.34	-0.3141	0.2539	-0.2257	10.38	R <sup>2</sup> neg.
0.41	0.39	41	-0.008	-0.004	-3.333	-1.86	1.2962	0.2682	0.6198	12.64	0.5765
3.88	3.67	(151)	-0.005	-0.003	-0.214	-.92	0.3545	0.3266	1.5289	12.89	0.8225
5.27	5.35	(138)	-0.002	-0.001	-0.063	-.40	* 0.3955	0.3522	0.8881	8.27	0.8323
3.58	3.63	(134)	-0.059	-0.028	-0.204	-.90	* 0.3972	0.3786	0.6357	11.43	0.6627
7.4	7.46	89	0.032	0.016	0.041	0.387					
7.3	7.18	—	0.030	0.015	0.035	0.320					
5.26	5.31	(96)	-0.002	-0.001	-0.064	-.41	0.5538	0.3120	1.2265	13.29	0.7730
5.61	5.70	(92)	-0.002	-0.001	-0.039	-.28	0.5783	0.3097	1.4007	14.92	0.7364
5.48	5.35	(103)	-0.002	-0.001	-0.056	-.36	0.5187	0.3375	0.6590	15.63	0.6240
3.82	3.83	78	-0.005	-0.002	-0.171	-.81	0.6875	0.3393	0.7891	15.04	0.8152
4.16	4.02	56	-0.004	-0.002	-0.123	-.66	0.9595	0.3217	2.9682	19.31	0.8014
7.74	7.75	(268)	0.022	0.009	0.044	.42	0.1987	0.3251	0.1643	8.78	0.7911
9.30	9.25	72	0.030	0.013	0.079	.91	0.7445	0.2948	0.2231	16.40	R <sup>2</sup> neg.
8.11	7.87	(233)	0.015	0.007	0.027	.24	0.2240	0.3432	1.0977	15.16	R <sup>2</sup> neg.
8.86	8.83	(119)	0.044	0.020	0.076	.88	0.4486	0.2650	1.0339	15.11	0.3934
3.24	3.39	52	-0.011	-0.005	-0.241	-.98	1.0240	0.3659	1.8079	16.97	0.7680
5.0	5.06	103	-0.040	-0.018	-0.027	-0.676					
6.3	5.90	112	-0.006	-0.003	-0.014	-0.108					
6.8	6.74	83									

Column 13 =  $\frac{1.6 \sum \text{eggs}}{3 (\text{computed } \sum \text{feed})} \times 100$   
 Column 14 =  $\frac{1.6 \times 100 \times \sum \text{eggs}}{3 (\text{computed } \sum \text{feed} - C. 22 \sum \text{gain})}$   
 Column 15 =  $\frac{1.6}{3 \times C. 20}$   
 Column 16 =  $.02083 \times C. 5 - .00123 \times C. 9$

Column 17 =  $\frac{C. 16}{C. 9} \times 1000$   
 Column 18 =  $.25 - .0143 \frac{C. 9}{C. 5}$   
 Column 19 =  $\left( \frac{C. 5}{C. 9} \times 33.75 - 2.00 \right)$   
 Column 23 = Sr = Standard error of estimate  
 Column 24 = R = Index of correlation

TABLE B.—TENTATIVE FEEDING STANDARD  
(Based on equation 8 in text)  
GRAMS OF FEED REQUIRED BY HENS OF DIFFERENT LIVE WEIGHTS.

No. Eggs Per Week	Body Weight, grams.															
	800	1000	1200	1400	1600	1800	2000	2200	2400	2600	2800	3000	3200	3400	3600	
0	43.7	50.1	56.1	61.8	67.4	72.7	77.9	83.0	87.9	92.7	97.4	102.1	106.6	111.1	115.5	
1	49.1	56.4	61.4	67.2	72.8	78.1	83.3	88.3	93.3	98.1	102.8	107.4	112.0	116.5	120.9	
2	54.5	60.8	66.8	72.6	78.1	83.5	88.7	93.7	98.7	103.5	108.2	112.8	117.4	121.8	126.2	
3	59.8	66.2	72.2	78.0	83.5	88.9	94.0	99.1	104.0	108.8	113.6	118.2	122.7	127.2	131.6	
4	65.2	71.6	77.6	83.3	88.9	94.2	99.4	104.5	109.4	114.2	118.9	123.6	128.1	132.6	137.0	
5	70.6	77.0	83.0	88.7	94.3	99.6	104.8	109.9	114.8	119.6	124.3	129.0	133.5	138.0	142.4	
6	76.0	82.4	88.4	94.1	99.7	105.0	110.2	115.2	120.2	125.0	129.7	134.4	138.9	143.4	147.8	
7	81.4	87.7	93.7	99.5	105.0	110.4	115.6	120.6	125.6	130.4	135.1	139.7	144.3	148.7	153.1	

Grams of "TDN" required for hens of different live weight.

0	32.9	37.7	42.3	46.6	50.8	54.8	58.7	62.5	66.2	69.8	73.4	76.9	80.3	83.7	87.0
1	37.0	41.7	46.3	50.6	54.8	58.8	62.7	67.6	70.3	73.9	77.4	81.0	84.4	87.8	91.1
2	41.1	45.8	50.4	54.7	58.9	62.9	66.8	71.6	74.3	78.0	81.5	85.0	88.4	91.8	95.1
3	45.1	49.9	54.4	58.7	62.9	66.9	70.9	75.7	78.4	82.0	85.5	89.1	92.5	95.9	99.2
4	49.1	54.0	58.5	62.8	67.0	71.0	74.9	79.8	82.4	86.1	89.6	93.1	96.5	99.9	103.2
5	53.2	58.0	62.5	66.8	71.1	75.0	79.0	83.8	86.5	90.1	93.7	97.2	100.6	104.0	107.3
6	57.3	62.1	66.6	70.9	75.1	79.1	83.0	87.9	90.6	94.2	97.7	101.3	104.6	108.0	111.3
7	61.3	66.1	70.7	74.9	79.2	83.2	87.1	91.9	94.6	98.2	101.8	105.3	108.7	112.1	115.4

Assumed weight of egg 55 grams.



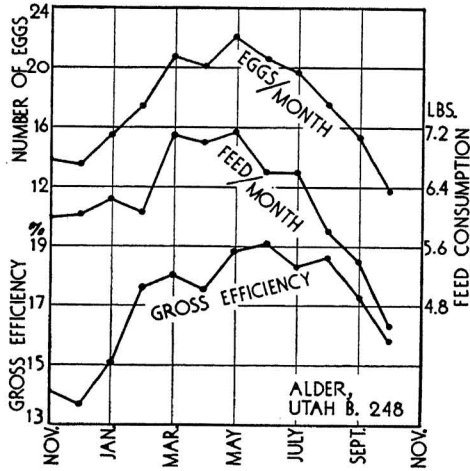


Fig. 13a.—The seasonal course of energetic efficiency of egg production (lower curve) computed by us from the Utah egg-laying contest data published by Alder, Utah Ag. Exp. Sta. Bul. 248.

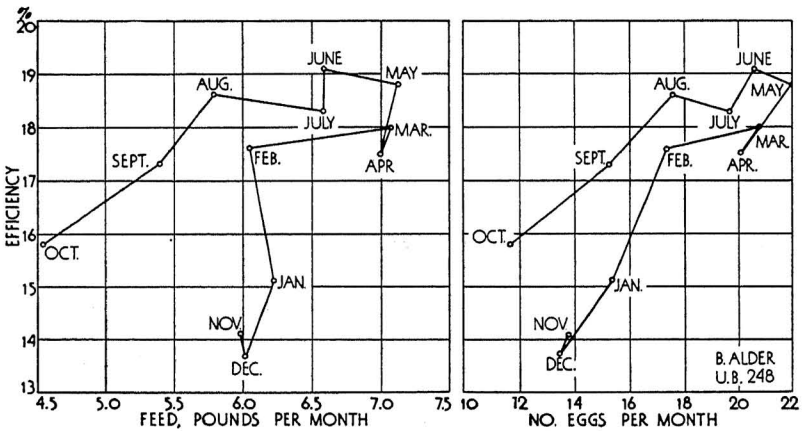


Fig. 13b.—The efficiency of the Utah egg-laying contest data plotted in another way. Why is the apparent efficiency during October (about 11 eggs) greater than during November-December (about 13 eggs)? Probably because we ignored in the computations the body weight changes.

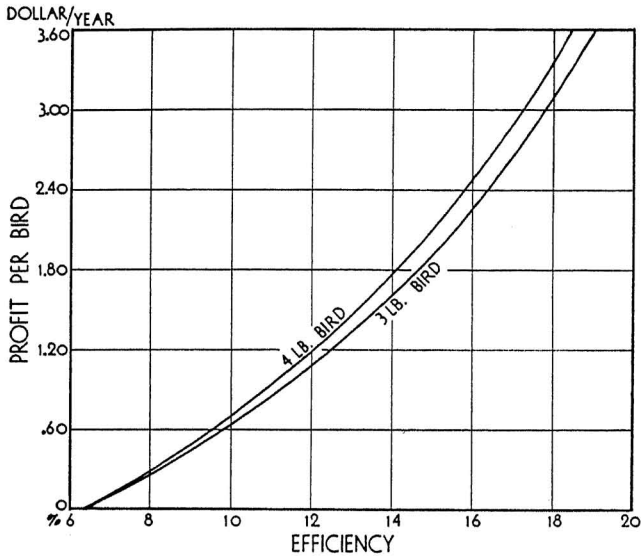


Fig. 14.—Influence of gross energetic efficiency on profit. This curve is a reply to a question "What is the influence of efficiency on profit?" The curves are based on the assumption that 56-grams eggs are sold at 25c a dozen and feed (containing 1360 Cal. TDN per pound) costs \$2.00 per 100 lbs., and that there was no other expense or income. Actually, about 10% of the income comes from sale of birds; and the expense for feed is perhaps only 50% of the total expense which includes labor (20-25%), replacement (10-20%), depreciation (8-10%), interest (4-5%), taxes (½%), etc. Note from this chart that according to these assumptions, it requires a 7% efficiency to cover feed cost, and that the profit increases more rapidly than the efficiency. Profit approaches infinity as efficiency approaches 100%.